HOME, WILLIAM SCOTT

ECOLOGY OF RIVER OTTERS (LUTRA CANADENSIS) IN MARINE COASTAL ENVIRONMENTS

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ECOLOGY OF RIVER OTTERS (*Lutra canadensis*) IN MARINE COASTAL ENVIRONMENTS

A

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William Scott Home, B. A.

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ECOLOGY OF RIVER OTTERS (*Lutra canadensis*)

IN MARINE COASTAL ENVIRONMENTS

RECOMMENDED:

Robert Elmer

Philip S. Gipson

P. A. Michelson

Chairman, Advisory Committee

Department Head

Director, Division of Life Sciences

APPROVED:

K. B. Cantor

Vice-Chancellor for Research and Advanced Study

December 23, 1982

Date

ABSTRACT

Otters or otter-like mammals arose several times from several sources in the evolution of the Carnivora. The probable steps in their adaptation to quatic environments can be traced with examples from the living Mustelidae. Most of the lutrine forms were associated with freshwater habitats, but some of them inhabited the maritime zone, as well. The seals (Phocidae) appear to have arisen from such a form. Other lutromorphic carnivores may have invaded the sea directly, withou previous aquatic adaptation in fresh water. The physical characters of Recent maritime mustelids were compared with those of related forms in inland habitats. The maritime forms tended to be largest and to have paler, coarser pelage than the others, but those were not consistent differences. Feeding and social behaviors were compared in a study of several groups of otters (Lutra canadensis) in lacustrine, marine, and intermediate habitats in southeastern Alaska. Those in the marine habitats were distinguished by much closer intrafamilial relations and more conservative use of space than for the other groups.

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I. INTRODUCTION

I.1. THE PURPOSE AND CIRCUMSTANCES OF THIS STUDY

A. Statement of Purpose

This study of the ecology and behaviour of marine-coastal pods of river otters in Alaska was structured along two basic axes:

(1) An investigation of the differences in foraging behaviour, social structure, and other activities, between the ecological group of seagoing river otters, and inland populations of the same species. In this I hoped to determine what, if any, adaptations were selected for in respect to these factors, in response to the special character of the maritime environment.

(2) An investigation of the factors in the ecology of seagoing river otters which tend to differentiate individual pods there into two habitual orientations: those factors which tend to reinforce habitual dependence, or reliance, upon marine waters for foraging and other activities, thereby reinforcing the tendency on the part of otters to become more specialised as aquatic mammals, with the eventual abandonment of any dependency upon terrestrial resources;

and, those factors which tend to reinforce the conservatism and the primitive generalisations of life habits and structure, which are evidenced repeatedly in the long history of otter lineages. These factors maintain a eurytopy of range exploitation and foraging strategies equally able to function on marine sea coasts, in complete dependence upon marine resources; in wholly freshwater, terrestrial ranges; or in coastal zones which necessitate a blend of the two strategies, proportional to the resources and character of the landforms and water bodies where the otters reside.

Both the marine-oriented and eurytopy-oriented tendencies have been recorded, in this study as elsewhere. Both develop and continue the evolutionary history of the otters as well as other lutromorphic lines, such as the phocids, otariids, and other mustelid subfamilies.

The specific ecological features investigated in this study, for the purpose of making the comparisons suggested above, were the following:

1) Foraging habits, and the relative use of eating activity sites, which demonstrate a correlation between the diversity of prey taken by otters, in proportion to the diversity of species available for predation.

2) Range size, and relative degree of utilisation of all parts of the range in all activities. The relationship of

landforms and substrate types to otter colonisation, relative use of the various types of substrate, water bodies, and specific rock or other features, and the activity budget in each type of substrate or water formation, was found to vary relative to the type of terrain included within each pod range. This was the principal factor reinforcing dependency upon a specific food base and therefore, the evolutionary strategy, as given above.

3) Social behaviour, which is reflected in some differences between inland and maritime otter populations, was monitored in view of the competition with other species of marine mammals. Special activities, such as vocalisations, cliff climbing, swimming and diving, and intraspecies interactions, were studied to determine whether these activities were modified by maritime residence. Social groupings and social-group activities were monitored to determine whether these activities provided an intermediate level of development between the same activities on the part of inland river otters and populations of entirely marine otter species (sea otters, chungungos). An intermediate degree in the evolution of these social systems was indicated for the marine-coastal otters. The data base of the present study is too limited for precise parameters of this differentiation to be defined at the present time.

B. Methods

The present thesis was compiled largely from the results of field studies conducted in the course of three separate projects. Anecdotal material has been added from other observations along the coast of southeastern Alaska, from Skagway to Ketchikan, from 1970 to 1978.

The three field projects were as follows:

(1) I was an employee of the National Park Service at Glacier Bay National Monument, Alaska, from 1970 to 1972. During this time, I collected data for a review study of all mammal species inhabiting the reserve, designed especially to compare the response of each species to range extension following deglaciation (a factor active in the Glacier Bay ecosystem on a rapidly changing, annual basis). Few formal studies of this aspect of the ecology were available in published literature. My sources consisted of field notes, log books, and file records compiled by previous employees of the National Park Service, particularly by Park Biologist Gregory Streveler. Unpublished field reports by earlier park biologists, such as Joseph Dixon, V. H. Cahalane, and others, were available only at park headquarters.

These records included detailed reports on discontinuous sites. Few studies were intensive, or long-term. Streveler had kept detailed records on the food habits of the otters in Bartlett Cove between 1967 and 1973.

I supplemented these records with my own observations in Glacier Bay proper, especially in Muir Inlet, as opportunities permitted. I collected all previous records of otters everywhere in the reserve, and conducted first-hand observations of the Barco pod (II.2, below), and those of Sebree Cove and Muir Inlet. I did not devote this study to otters exclusively.

Because of the diversity of the sources used in this work, I will cite all information derived therefrom as "Home, 1973." Persons interested in the specifics of the various species accounts may consult this source for more precise documentation.

(2) In 1973, I contracted with the Cooperative Park Studies Unit, University of Alaska, to conduct an ecological survey of the overwintering mammals and birds of the Dixon Harbour/Boussole Bay area on the Pacific coast of the national monument. My winter study was only one aspect of an intensive, year-round ecological investigation conducted by a team of scientists. My winter observations were supplemented during the summer by those of others. The combined studies provide the only information on year-round activities of seagoing otters in southeastern Alaska.

I resided in a field camp located in Thistle Cove, at the north end of Dixon Harbour, from 20 November and 20 March, 1973-74, and from 20 October to 9 May, 1974-75. The otter pod resident in Thistle Cove was under observation almost daily, especially during the second winter.

Activities undertaken in the collection of data were as follows:

(1) I made daily foot patrols (boots or snowshoes) throughout the area of the Dixon Valley and Boussole Valley. The rock face and gravel shore of Thistle Cove I inspected daily for all signs of mammal activity, tracks, feeding remains, and scat. I was able to record observations of the otters' behaviour.

The Dixon valley was visited every four to five days. The Boussole valley was investigated on an average of every three days. At some times, successive daily visits were made.

Different routes were followed on successive days, in order to maximise coverage of the entire area over a monthly basis. Fig. 1 shows the map of the study area with the total number of transect routes marked. Areas of repeated investigation and frequent crossing at all transects are indicated by shaded lines. Single lines extending from these areas mark routes taken as infrequently as once or twice a month. Weather was often a limiting factor.

At the end of the second winter, I had covered the entire area to a degree beyond the limits of either pod's range or activities. I was able to define these limits by mapping my daily observations and correlating these with the activity patterns of all mammal species occurring in the study area.

(2) I investigated the rock face of the coast to the south of Thistle Cove by sport-yak, when weather and water conditions permitted. Much of the sheer, irregular cliff was inaccessible either from water level or the summit above, because of the swell of the harbour's water. Only three visits were possible in each winter. Although the resident pod maintained its habitual winter den in this cliff, I was unable to examine it closely.

(3) I collected scat wherever it was found. All scat was packaged and treated with preservatives in camp. Most of the contents of the scats could be determined in camp, because of my familiarity with the invertebrates consequent to my previous studies of the invertebrate faunas of Glacier Bay. Identification manuals issued by the Universities of Washington and of British Columbia were available at Bartlett Cove. Prey items which could not be identified by these sources were referred to the reference collection of specimens, maintained by Streveler at Bartlett Cove, and to other taxonomic keys secured by interlibrary loan.

I was active around the two altars in Thistle Cove, and other preferred eating sites, throughout the study. The Thistle pod made little use of these sites during the winter, for this reason. It was necessary to inspect the rock and gravel shore frequently in order to census prey remains before they were removed by the tide, since most feeding remains were left at random points around the shore.

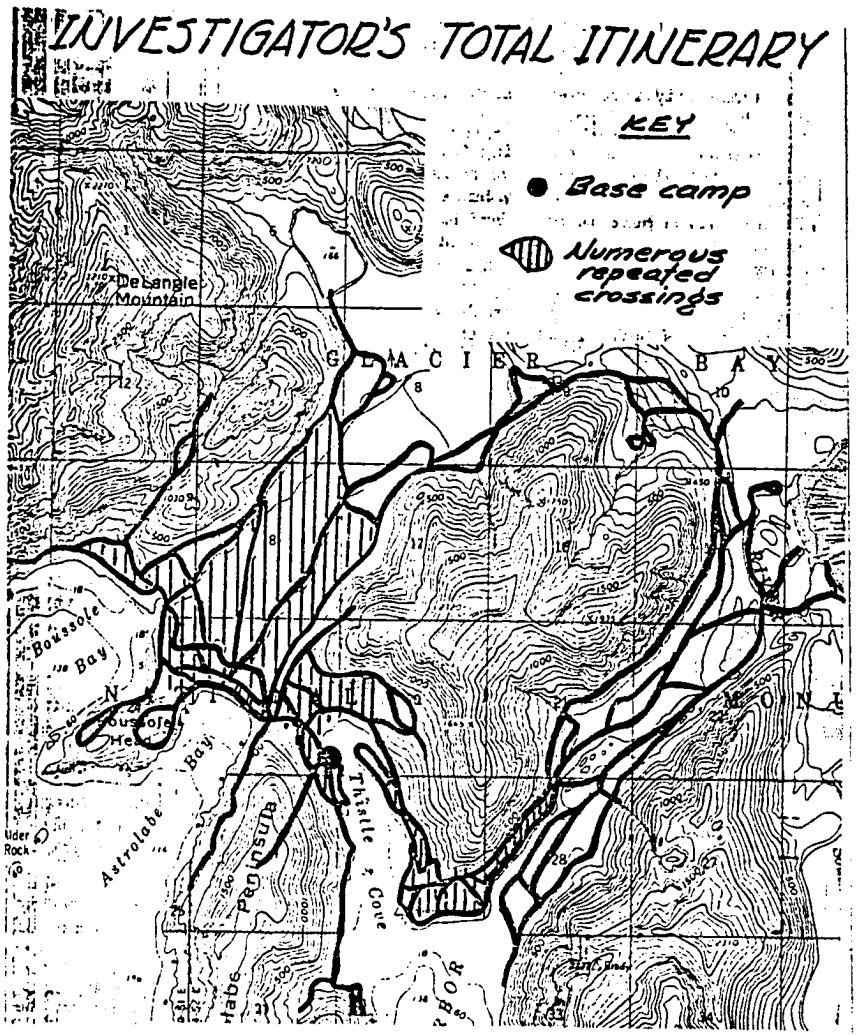

FIG. 1. INVESTIGATOR'S TOTAL ITINERARY

WINTER STUDIES, 1973-1975

No habitual feeding sites were located either winter or summer for the Boussole Valley pod. Probable reasons for this are discussed in II.2, below.

This material, collected during the Dixon Harbour Biological Survey (1973-1975), was originally discussed elsewhere (Home 1977). Details of operational methods, and factors in the ecological variations observed over the two winters, may be obtained from the original report. However, this thesis contains data derived from, but not included in, the original report.

(3) In summer, 1978, Park Naturalist Bruce Paige secured me a grant from the Volunteers in Parks program. I was able to carry out hydrophone acoustic studies of the marine mammals and other animals in the waters of Muir Inlet, with equipment supplied by W. H. Lawton (University of Washington, Seattle). The terms of the contract permitted me to spend weeks during July and August in intensive daily monitoring of the otter pod at Goose Cove. The log books kept by field rangers stationed in Goose Cove during all summers since 1969 were still available. A useful body of long-term comparative data for this pod is thus available.

In addition to the Goose Cove observations, and the hydrophone surveys, conducted at many sites in Muir Inlet and Adams Inlet, I investigated the coast and waters adjacent to Goose Cove and Sealer's Island by kayak. Other kayak trips were made, as circumstances allowed, to the coast occupied by otters at

Rowlee Point, Sebree Point, and Adams Inlet. Studies sufficiently detailed to determine range limits and behaviour of these three pods were not possible, however. But scat was collected on all trips.

I discovered that the collection of scats recently deposited, or of any frequent activity on my part around feeding sites habitually used, tended to disturb or displace the otters using those sites. I thus limited my collections of scats to the days at the conclusion of the study period. Scats therefore had to be censused at the time of discovery, whether collected or not.

An index collection of scats was returned to the lab in Bartlett Cove to be oven-dried, weighed, and examined. I added no preservatives to these specimens.

I walked the coast north and south of Goose and Nunatak Coves, the west coast of Muir Inlet, and the coast of Adams Inlet, to examine the sites of otter activity. Most of the material derived from these peripheral investigations is introduced as anecdotal in this study.

In addition to the three intensive studies, above, I made limited, short-term studies on otters at Etolin and Brownson Island, summer, 1977, in the course of an ecological survey I conducted for the U. S. Forest Service, Petersburg District. Other observations were made, incidental to other studies, at Indian Point, near Juneau; the mouth of the Taiya River, west of

Skagway; and in the Sitka Narrows, north of Sitka.

Dr. David Hatler (Northwest College, Terrace, B.C.) has kindly communicated to me unpublished results of his observations of otter pods on Vancouver Island, and other islands on the coast of British Columbia. The number of parallels between my own observations and those of Dr. Hatler suggest that much of the material presented here is not just a sample, but is typical and representative of otters in these two separated segments of the North Pacific coast.

Material from the remaining references was collected during my residence at the University of Alaska, 1976-1979.

C. Definitions

Many specialised terms pertaining to the details of otter ecology have evolved in the English language. Such terms are commonly encountered in the British literature (e.g. Stephens 1957, Harris 1968), but few are defined in standard references. I have avoided using them, except in direct quotations, and have substituted conventional zoological terminology. The following are the principal emendations:

Terminology in litt.	Terminology herein
Dog otter	Male
Bitch otter	Female
Pups	Kits

Seals	Tracks (footprints)
Holts	Dens
Spraints	Scats
Ottery	Focal water (II.1, below)

The otters which are the subject of this thesis form a distinct ecological set which has not previously been identified by a diagnostic term.

In Scotland, maritime otters are called "sea otters" (Fraser, in Tetley 1945), or "littoral otters" (Elmhirst 1938). In this paper, the term sea otter is used only for Enhydra lutris. The term "marine otter" was suggested by Simon (1966) for the chungungo, Lutra felina, of western South America. That name has been used broadly and indiscriminately. The name chungungo will be used for that species throughout this study.

Maritime, or marine-coastal otters whether in Britain, Russia, China, or the Americas, seem, as a group, to be distinguished by characteristics unlike those of inland populations of the same species. Such distinctions are true of several different species of otters around the world. Individual factors, such as body size and colouring, also vary between maritime and inland populations. Delineation of these characteristics is the subject of a part of the present study. Because of the ambiguity inherent in such terms as maritime otter, marine otter, littoral otter, sea otter, etc., I

propose a specific term for all these maritime populations: kushta otter. The word kushta is the proper name of river otter in the Tlinkit language. Tlinkits know these otters chiefly as seagoing mammals.

I will use the term kushta otter throughout this thesis for Lutra canadensis and L. lutra, to apply to all individuals which exist on or near coastlines and make daily (or at least very regular) excursions into the sea for foraging purposes, on a year-round basis. Otters which venture to the sea only occasionally are not included in the term. There is no evidence from the coast of Alaska or British Columbia that these otters undergo any major changes in range on a seasonal basis. Evidence of seasonal change in the range of British and other kushta otters seems doubtful, in view of the data available from specific studies (I.3, below).

Kushta otters den along sea cliffs and coasts, and on rivers and lakes with access to nearby coasts. These otters maintain feeding and defecation sites particularly around salt water beaches. Kushta otters forage at sea in competition with seals, sea birds, whales, and mink, and on shore and inland with other competitors, such as wolverines and weasels. Otters are sometimes preyed upon by eagles, and may be subject to predation by terrestrial carnivores. Many of the otters in my study did not venture more than 100 m from the shoreline at any time in their activities.

I do not extend the term kushta otter to include any pod which occupies a river, or adjacent waterway, but does not enter

the sea even if this river is flooded at high tide. The Gustavus pod (II.1, below), which never ventures to the coast or into salt water outside the river channel, is not a kushta pod, even though its progeny of necessity interbreed with kushta otters of neighbouring pods.

For the sake of consistency, the following vernacular names will be used in this paper (in addition to the diagnostic names given above):

Sumpfotter (=European mink)	Mustela lutreola
Mink (=American mink)	Mustela vison
Saro (giant otter)	Pteronura brasiliensis

I.2. THE EVOLUTION OF MARITIME FISSIPEDS AND MUSTELIDS: THE LONG HISTORY OF THE OTTER-LIKE BODY AT THE EDGE OF THE SEA

A. Early Marine Lutromorphs

The lutromorphic body is a somatic adaptation to aquatic exploitation. The characteristics distinctive to this body appeared earlier in mammalian evolution than did the subfamily Lutrinae. An otter-like body is presumed for the ancestors of both groups of modern pinnipeds; the ancestor of the phocids probably was an otter (B, below). The Lutrinae, as a group, have retained anatomical primitivisms despite repeated adaptations to marine habits in the past ten million years. Such somatic conservatism, including retention of a primitive dentition originally classified as fish-eating, but in fact suitably omnivorous, has been selected for, particularly in coastal and pericoastal habitats.

Many aquatic species of insectivores, rodents, artiodactyls, and other orders, which appeared throughout the Tertiary, are still common around the world. It is natural to assume that lutromorphic mammals appear on seacoasts, or in oceanic habitats, only after a long period of aquatic adaptation in freshwater bodies. This need not be the case. To date, there is no fossil evidence for freshwater precursors of the family Enaliarctidae. Mammals principally freshwater in origin may have

become active in estuarine and coastal environments from very early in their appearance on the evolutionary scene. There is evidence for this among the earliest of aquatic mustelids (B, below).

The transition from freshwater to saltwater exploitation probably involved little time delay for any species already adapted to aquatic activity. Modern otters taken from freshwater ranges have been introduced to the salt water of cold oceans without giving any evidence of problems in the course of becoming regular salt-water swimmers and divers. Temperature, rather than salinity, was the impediment to these otters, and they adjusted to it quickly. Both the Iraqi and Nigerian otters which Maxwell (1960) transported to the north coast of Scotland were originally inhabitants of estuarine environments - the Tigris and the Niger. It is possible that each otter came from a population with long experience of saline or brackish water.

But mink have also been transplanted from inland ranges in North America to maritime habitats in Eurasia. Some of these adjusted to saltwater foraging within the lifetimes of single individuals (D, below).

The mustelid family arose, at the beginning of the Oligocene, from primitive arctoids. The oldest known form is the 36-million-year-old Mustelictis (Radinsky 1971). In subsequent years, the family produced "small, marten-like" forms (Kurten 1972) such as Plesiogale, Paragale, and Promartes (Radinsky 1971). These were presumably forest-dwellers.

But "small, marten-like" forms today - to wit, the marten (Martes americana) - descend to the intertidal zone to forage, during low tides, in the Queen Charlotte Islands (Foster 1963) and on Kayak Island, Alaska (F.H. Fay, Institute of Marine Sciences, University of Alaska, pers. comm.) without compromising their arboreal habits. Marten often make beach forays along the coasts of southeastern Alaska, when the populations of small mammals which are their usual prey decline inland (Home 1977). Such responses to fluctuations of prey populations could produce a swimming coastal forager in a fairly short time, particularly if such a mammal encountered none of the competition which modern martens experience from otters and mink, and if it found no phocids or otariids waiting in the water.

Today, in the biogeographic "islands" of the Alaskan coast (II.1, below), isolated by water both liquid and frozen, almost all large and small mammal populations inject individuals into new ranges by swimming. The crossing of glaciers is a relatively rare strategy. All mammal species occurring in contemporary southeastern Alaska - moose, mountain goats, brown and black bears, deer, wolves, lynx, rodents, and even water shrews - have been seen swimming in salt water (Home 1973, 1977). Even boreal toads paddle there.

This forced assumption of swimming habits, which influences even such hydrophobic species as wolverines and porcupines, could have been decisive on the activities of early proto-bears or proto-mustelids. Coastal foragers may have evolved without freshwater intermediaries.

Such primitive mammals may initially have engaged in the "semidives" (IV.5, below) I have observed among modern unspecialised otters. From an intertidal forager and imperfect swimmer, such as a marten, might develop a short-term swimmer and waterline forager, such as a mink. Modern mink are not good fishers (Erlinge 1968), but adaptations which improved fishing or crustacean-hunting would reinforce an orientation to habitual pursuit of benthic and nektic prey. A mink so "improved" would become an otter.

Once the new mammal's body had become modified to undertake longer dives (by adapting to a greater degree of oxygen deprivation), a complete adaptation to the modern marine environment, equal to that of the modern marine otters, would have been achieved. Phocids and otariids underwent further development, transforming their limbs into flippers. This specialisation defines the boundary between lutromorphy and phocomorphy. Sea otters, as well as other marine otters past and present (cf. below), achieved near-total marine adaptation while remaining lutromorphic - without modifying the limbs.

The marshy lakes and streams of the Eocene forests of Wyoming provided the habitat of a primitive aquatic mammal which Bruce (1883) designated Megencephalon, and assigned to the Lutrinae. This mammal has never been restudied, and is not mentioned, even as a synonym, by Scott (1937), Simpson (1945), or Romer (1966). Savage (1957) observed that it was not only no otter but not even a fissiped.

He did not doubt its anatomical convergences with otters, but did not suggest where its relationships might lie.

This is the first appearance of the lutromorphic body in the known fossil record. Other arctoid lineages evolved similar forms after the Oligocene. The most significant of these, discussed in the following sections, are diagrammed chronologically and phylogenetically in Fig. 2.

The hemicyonine ursids produced at least one, and probably many more, lutromorphic lineages from which the enaliarctids and otariids evolved (Mitchell and Tedford 1973). The proto-phocid was probably related to the first otter, Potamotherium, which gave rise to a lineage of large marine otters (B, below). Potamotherium was more specialised, aquatically, than the ancestral stock of the modern Lutrinae, which thereby constitute a distinct lutromorphic lineage - perhaps more than one (C, below). The modern Mustelinae have also produced several distinct lutromorphic genera (D, below). Even the Old World viverrids produced such lutromorphs as the otter-civet, Cynogale benneti (Medway 1969).

It is probable that American hemicyonines had begun to exploit the seas at an earlier date than the Old World lutrines. As early as 1885, Mivart pointed out osteological and anatomical parallels between Lutra and Phoca, and between Otaria and Ursus. These relationships have been confirmed, not only from anatomical evidence, but by serological studies (Sarich 1969a, b). The time scale calculated from serological data for the divergences tends to

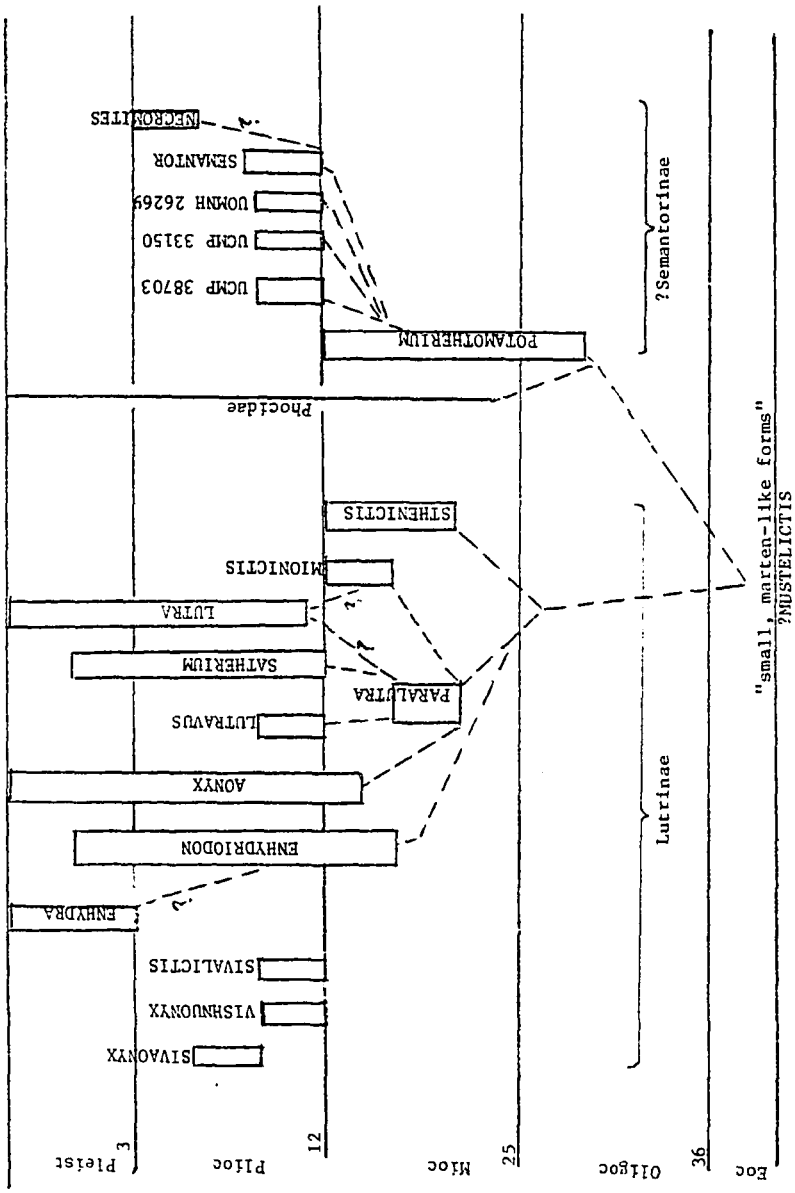

FIGURE 2

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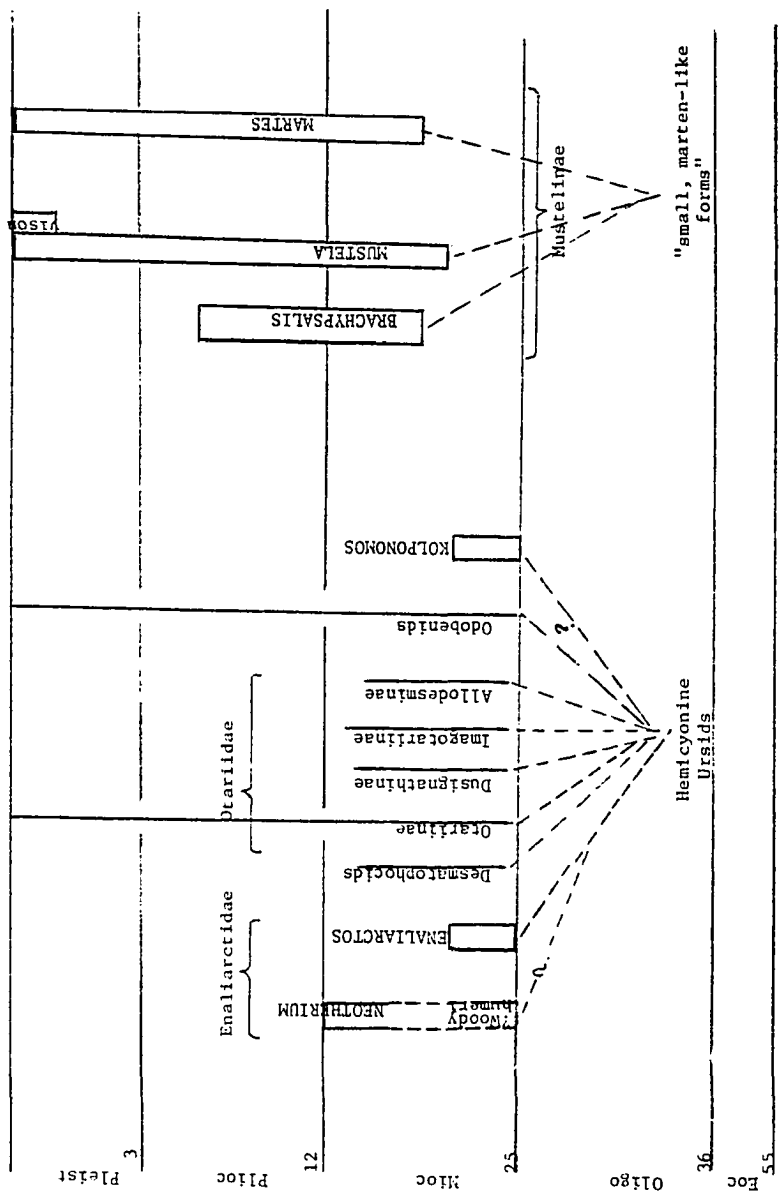

FIGURE 2

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a shorter interval than is indicated by fossil anatomical evidence. The discovery of Enaliarctos (Mitchell and Tedford 1973) in the early Miocene of California provided the first genus intermediate between ursids and otariids, supporting Mivart's early insight. This genus could be classified equally well in either the Ursidae or the Otariidae (Mitchell and Tedford 1973), but is sufficiently distinct from both to be allotted family status of its own (Repenning 1976a).

No Oligocene record of maritime or aquatic hemicyonines is known. By the earliest Miocene, no less than eight, and possibly more divergent hemicyonine lineages were established within completely marine environments in the North Pacific: the enaliarctids, desmatophocids, and otariine, dusignathine, imagotariine, and allodesmine otariids (Mitchell and Tedford 1973), as well as Kolponomos (Stirton 1960), and otariid or enaliarctid kin (Ray 1976b), and odobenids.

Obviously a wildfire adaptive radiation was under way. This suggests that neither Megencephalon nor any other mammal had produced any competitors which could exploit the Oligocene-Miocene seashores. Exploration of such coastal habitats must have become common among ursids long before the beginning of the Miocene.

Given the temporal gap between Enaliarctos and the other otariid subfamilies, and taking into account a variety of still-unclassified forms (below), the lutromorphic body and habitus must have been produced many separate times, tending, in each case, to the evolution of an increasingly marine (phocomorphic)

mammal. In most of these, the forelimbs were converted into flippers.

Enaliarctos, although a late offshoot of the ancestral otariid stock, was only slightly larger than the living Lutra (Mitchell and Tedford 1973), yet probably had flippers (Repenning 1976b). This makes it probable that the proto-enaliarctid was of much the same size, appearance and habits as the contemporary kushta Lutra. Through developmental stages unknown in the fossil record, Enaliarctos's parallel and contemporary, Potamotherium, had already become highly modified for aquatic life in Europe (B, below). Such structural modifications must have begun to evolve in the early Oligocene.

In the earliest Miocene, Enaliarctos competed with other otariids as the last exemplar of the stock from which all were commonly derived. Enaliarctos retained its fissiped dentition, and probably carried its food ashore to eat (Repenning 1976b). Mitchell and Tedford (1973) noted, ". . .isolated bones from marine Miocene rocks in the North Pacific (25 to 22 million years ago) indicate that there were many species of aquatic carnivores of otter or pinniped habitus that have not been described," and "it is obvious that a large number of aquatic fissipeds must have existed in the early or middle Miocene, most of them still poorly known."

These diverse, and still unstudied, bones indicate that the family Enaliarctidae was widespread in several differentiated forms from 22 to 16 million years ago, around the North Pacific (Tedford 1976). The waters of the early Miocene coast of California were warm moderate to deep, and contained cetotheres

and other mysticetes, squalodonts, deep to mid-water fishes, sea turtles, deep-water sharks, as well as dusignathine, allodesmine, and imagotariine pinnipeds, over mud and sand bottoms. The invertebrate fauna was much the same, in broad taxa, as that of warm waters farther south today (Mitchell and Tedford 1973).

A high degree of aquatic competition sharply modified the ursid cranial characters of Enaliarctos. That it had flipper limbs assumed on the basis of isolated humeri (Repenning 1976b), is not yet confirmed. Its skull had an enlarged narial chamber, reduced olfactory bulbs, a wide muzzle, a long, hard transversely arched palate, tendencies toward premolarisation of the molars, a narrow interorbital region, good arterial supply to, and an enlarged venous drainage of, the skull - all specifically aquatic modifications, and all features possessed at some stage in the evolution of each of its kindred groups (Mitchell and Tedford 1973).

Another possible enaliarctid, Neotherium (Kellogg 1931), known certainly from Allodesmus beds of the late Miocene, may be represented by some humeri, calcanei, an astragalus, a navicular, and femori (Downs 1956), from the Woody formation. Originally, Wilson (1935) described these remains as otariid. Mitchell and Tedford (1973) believed that Neotherium, still poorly known, may be a marine fissiped. This would not argue against its enaliarctid affinities. Neotherium's humerus is like but distinct

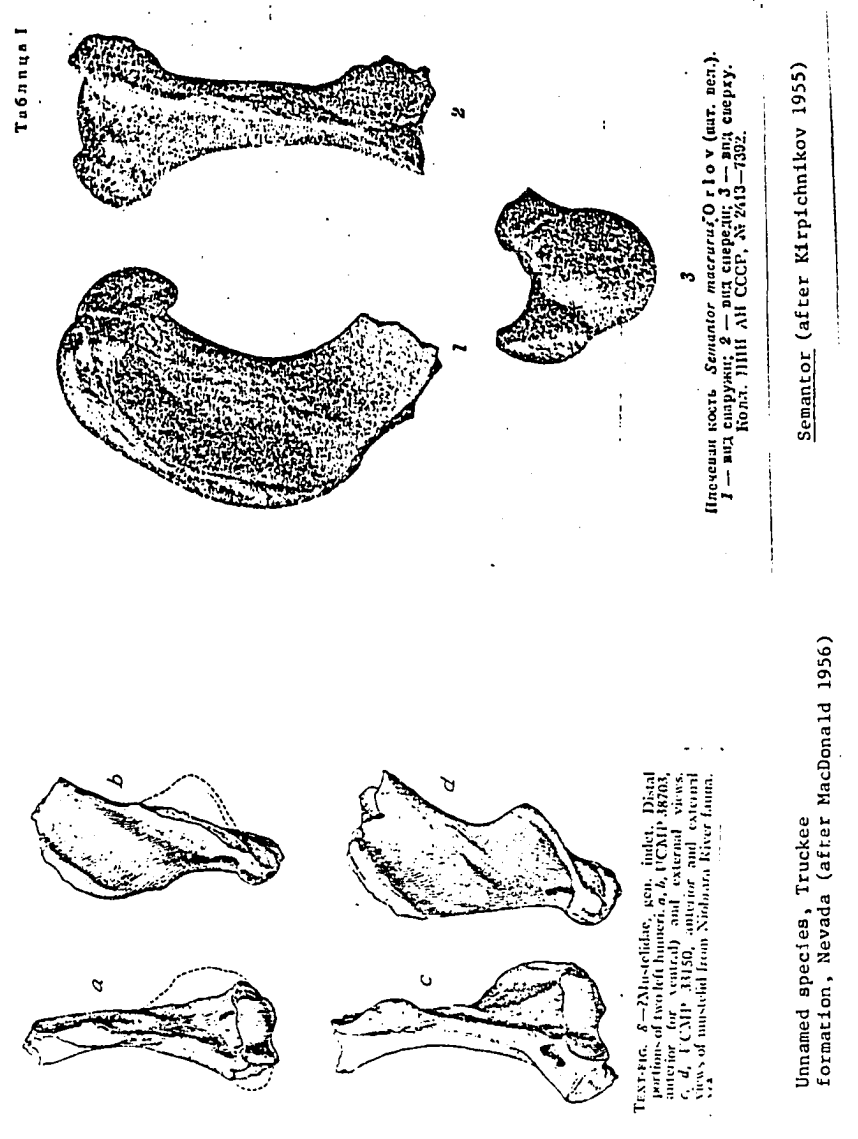
from, that of otariids of the same period. It bears some resemblance to Kirpichnikov's (1955) supposed Semantor humerus (Fig. 3). In this, a degree of convergence may be supposed.

B. Potamotherium and Its Legacy

Serological studies have indicated a close affinity between ancestral phocids and otariids (Sarich 1969a, b). Mitchell and Tedford (1973) believed there is a genetic relationship, and not simply parallelisms, between Enaliarctos and Potamotherium valletoni. Tedford (1976) pointed out that the characteristics of Potamotherium "are a mixture of arctoid features, which makes it difficult to assign (it) to a specific family." Tedford considered Potamotherium a link between mustelids and phocids, equivalent to the link Enaliarctos provided between the ursids and otariids.

The earliest known phocid is from 22-million-year-old Himalayan rocks of the Tethyan-Paratethyan seaboard (Ray 1976a). Both phocine and monachine seals were in existence by the late early Miocene (Ray 1976a). Tedford (1976) considered the resemblance between young adult monachine skulls and the skull of Potamotherium "amazing." A concept of the proto-phocid may thus be obtained by examining Potamotherium itself.

The first phocid achieved a level of marine adaptation equal or superior to that of Enaliarctos, at about the same date as Enaliarctos. A similar process of maritime habituation through



TEXT-FIG. 8—Mustelidae, gen. indet. Distal portions of two left humeri. *a, b*, UCMP 38703, anterior (or ventral) and external views. *c, d*, UCMP 38150, anterior and external views of mustelid from Niobrara River fauna.

FIG. 3. PLIOCENE HUMERI OF "SEMANTORINES"

(Continued

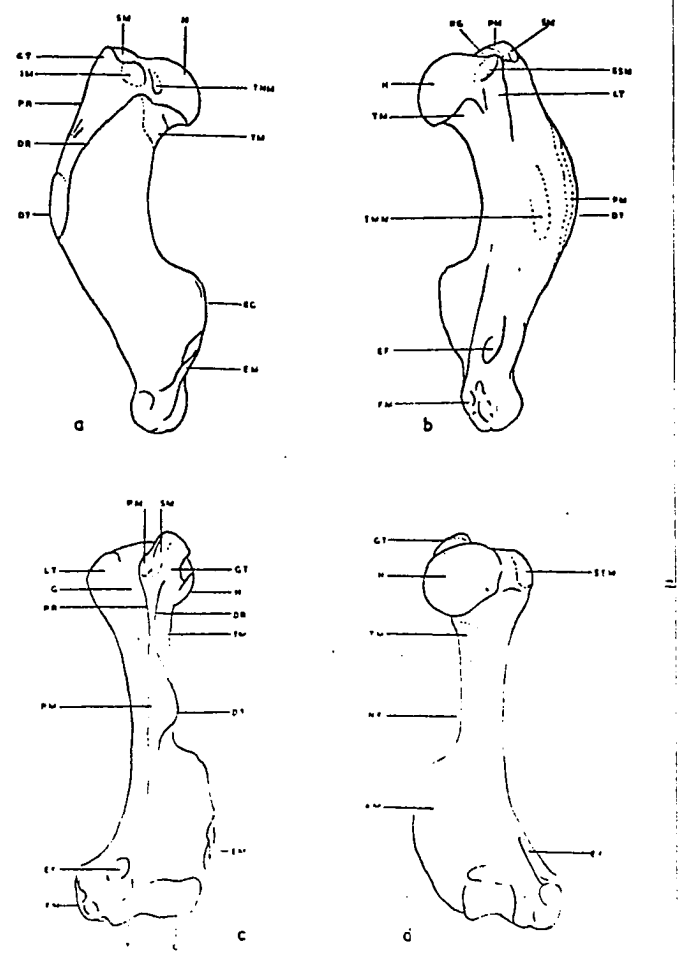


Fig. 22. *Potamotherium valletoni*. left humerus; ×1. Modified by approximately natural size. a, Lateral view; b, medial view; c, anterior view; d, posterior view. AM, anconeus muscle; Bi, bicipital groove; C, coronoid; DM, deltoid muscle; DR, deltoid ridge; DT, deltoid tuberosity; EC, ectepicondyle; EF, entepicondylar foramen; EM, extensor muscles; FM, flexor muscles; GT, greater tuberosity; H, head; IM, infraspinatus muscle; LT, lesser tuberosity; NF, nutrient foramen; PM, pectoral muscles; PR, pectoral ridge; SM, supraspinatus muscle; SSM, subscapularis muscle; T, trochlea; TM, triceps muscle; TMM, teres major muscle; TNM, teres minor muscle.

Potamotherium (from Savage 1957)

FIG. 3. PLIOCENE HUMERI OF "SEMANTORINES"

the late Oligocene by a Potamotherium-like animal (or even by a species of this genus) may be indicated (Ray 1976a). Unlike the hemicyonine experiments, only a single lineage seems to have survived.

Potamotherium appeared late in the Oligocene (Savage 1957). Although it is usually classified as a lutrine, the genus shows no sign of the same arctoid origins as other mustelids (Radinsky 1971). Savage (1957) considered this lutromorph an inhabitant of freshwater, only. Yet the map Savage provided to illustrate the distribution of Potamotherium through Oligocene water bodies indicates that the animal had opportunities for extensive contact with the sea in brackish lagoons (Fig. 4). The most abundant remains of Potamotherium were thus associated with lakes north of the Rhone valley, but as much as 20% of the known fossils have been found in deposits originating from brackish lagoons (Savage 1957). Potamotherium may thus have broached the sea at a date sufficiently early to be a contemporary with that of the proto-phocid.

Potamotherium, and the probably related Semantor, are considered "possibly the only real intermediate between land and sea adaptations" (Ray 1976a). The skull of Potamotherium is more primitive than that of contemporary Oligocene mustelids, even Mustelictis (Radinsky 1971). The lineage from which Potamotherium arose must have diverged from the basal mustelid stock before the earliest known fossil forms (Radinsky 1971). There is undoubtedly, a gap of major proportions in the early fossil record

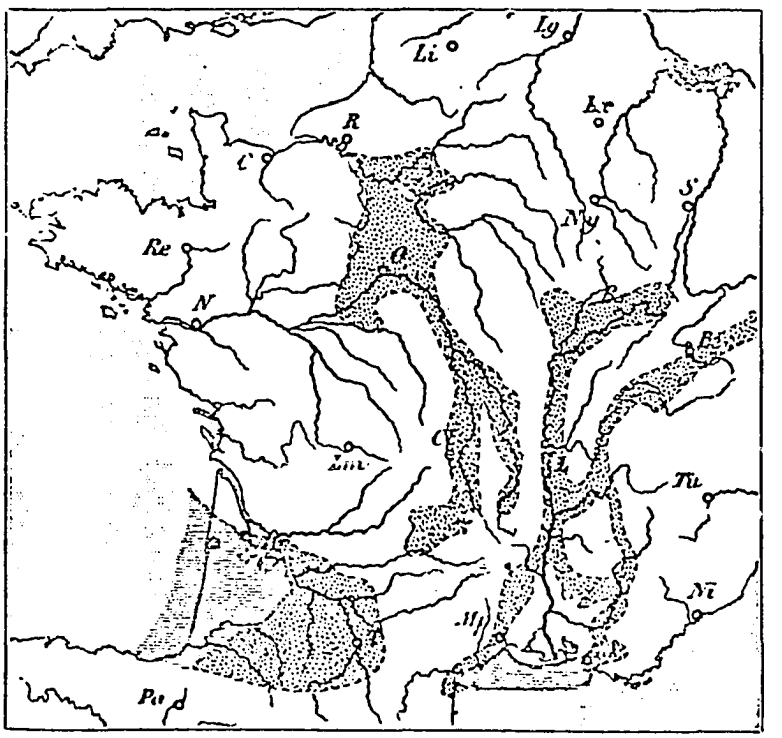


Fig. 1.—France in Aquitanian (Upper Oligocene) times. White=land. Dotted areas=lakes or lagoons. Ruled=sea (after de Lapparent).

FIG. 4. OLIGOCENE DISTRIBUTION

OF POTAMOTHERIUM

(from Savage 1957)

of the family.

This is indicated by the fact that evolution of the craniate sulcus, which Radinsky (1971) believed had occurred independently in five separate. but parallel, lineages, had a common feature in all of these not yet traceable to a common ancestor. Surely it is more reasonable to assume a single, not yet discovered, predecessor, which initiated the sulcate trend. Such an animal may finally bond together the lineages of Potamotherium, the phocids, and the subsequent mustelids. Given its four-million-year "jump" on the first phocid, it is not impossible that Potamotherium itself was the proto-phocid.

Potamotherium was the largest mustelid of its time, and exhibited the greatest ratio of brain volume to body size, and the greatest differentiation of the cerebral surface, of any mammal in its environment (Savage 1957). Such mustelid contemporaries as Promartes, Paragale, and Plesiogale were 1/2 to 3/4 the size of this first otter (Radinsky 1971), which was itself the size of the living Lutra (Savage 1957).

The inland lakes in which Potamotherium was most common were small and shallow, and surrounded by broad belts of marsh. The mammals, birds, and reptiles associated with that earliest otter made up an assemblage suggestive today of an African environment (Savage 1957).

Anatomically, Potamotherium was more specialised aquatically than the living Lutra. Lutra must be similar to Potamotherium's predecessor. The teeth of both genera are similar

but Potamotherium was "more primitive" in its trend toward premolarisation - an aquatic character (Savage 1957).

The skulls of both genera were about the same size, but the orbit is larger in Potamotherium, and the dorsal flattening of its head more pronounced than in Lutra. This flattening enabled the earlier otter to survey the water surface with only minimal exposure of its head. Evidently Potamotherium could close its nares underwater.

Like Lutra, unlike the phocids, Potamotherium had a chewing, not a catching jaw. In the facial region, Potamotherium's cranial circulation was "primitive;" probably it had a poor sense of smell. The respiratory turbinals were large, unlike those of monk seals.

The reduction of the spines on Potamotherium's post-thoracic vertebrae exceeds that of the modern sea otter, and approaches that of Otaria. In Otaria this reduction is associated with fore-limb propulsion; Potamotherium has been presumed to share the hindlimb, or posterior-somatic, propulsion of Lutra and the phocids.

But Potamotherium's forelimbs were capable of a powerful backward drive, and were as good for digging as for swimming. Half the bones in the forelimb resemble those of Lutra, the other half those of Phoca. Savage (1957) believed that the forelimbs were held against the body in swimming, the manus being used for steering in the manner of modern phocids and of Lutra. He believed

propulsion was supplied by the hind feet, the digits of which were longer than in Lutra, probably were webbed, and had a large "paddle area." On the evidence of the mixed characters, Potamotherium may have been equally adept at forelimb or hindlimb propulsion, and at present, it is difficult to determine which may have predominated.

Like the sea otter, and phocids, Potamotherium had a short tail; Lutra has a longer one.

Savage (1957) believed that Potamotherium came ashore less often than Lutra, and felt that the genus combined the sagittal flexibility of Lutra with the lateral flexibility of Otaria. Potamotherium, like Phoca, respired chiefly by rib movements, and was adapted to staying under water longer than is Lutra. The pelvis indicates that Potamotherium probably bore only one or two offspring at a time, more developed at the time of birth than are Lutra kits. This is another aquatic specialisation, and a trend toward Phoca.

On land, Potamotherium resembled Lutra - at least, the smallest living species, Lutra felina - though it had short, stocky legs, and could, perhaps, barely lift its head off the ground. Its arched back rose above the level of its head. In its short hops it may have made slower progress than Lutra (Savage 1957).

Savage suspected that Potamotherium was more lacustrine than fluviatile, so that, despite nearly ten million years of successful survival as the most aquatic and most cerebral of mammals, the entire population died out as the Aquitanian lakes

disappeared. But it did not die out. Other, larger species such as P. miocenicum, survived into the late Miocene in Europe (Jong 1972).

The basic stock of the Mustelidae originated in the Old World (Radinsky 1971), and moved into the New World in recurrent waves. At least one invasion occurred in each successive epoch (Scott 1937). Until the Pliocene, the family was more abundant in Eurasia than in America. Oligocene Europe had an abundance of both mustelids and viverrids, while contemporary North America had very few (Scott 1937).

Potamotherium appeared in the New World after the earliest phocids had begun to spread along Old World coasts, and at least five otariid-odobenid lineages had died out in the Pacific, while three more had become established there.

Endocranial casts, humeri, and other, smaller bones of an animal resembling Potamotherium have been found in several early Pliocene sites of western North America. Although dissociated, the bones not only show affinities with Potamotherium, but differ from it only by an increased degree of aquatic specialisation. These animals were associated with rivers as well as lakes (MacDonald 1956); some were estuarine (Orlov 1931, 1933).

A ten-million year-old endocranial cast from Oregon (Univ. Ore. MNH 26269) compares not only with Potamotherium, but with phocids, in general profile, in the forepart of the brain and in the position of the stumps of the olfactory bulbs (Radinsky 1968).

Two isolated humeri resemble that of Potamotherium, and may have originated from the same species as the endocranial cast mentioned above. One of these is from the late Miocene/Pliocene

Truckee formation of Nevada (UCMP 38703). The other, specifically distinct although otherwise similar, was found in the Niobrara formation of Nebraska (UCMP 33150). Each of these humeri is broader and flatter than those of Potamotherium valletoni (Fig. 3). Otherwise the resemblances are close (MacDonald 1956).

Comparison of these two humeri with that of Potamotherium and the supposed Semantor humerus of Kirpichnikov (1955) suggests relationships among them (Fig. 3). The genetic grouping, acknowledged indirectly by Tedford (1976), seems to be supported.

In Nevada, this unnamed species was riverine, and was sympatric with two true lutrines of more recent origin, Lutra and Lutravus, the former in its first appearance in the New World (MacDonald 1956).

Semantor macrurus (Orlov 1931), from the early Pliocene of the vast Sarmatian basin, is so far known only from the rear half of a single skeleton found in the banks of the Irtysh river (Orlov 1931, 1933). Savage (1957) considered the similarities between Potamotherium and Semantor "astounding." Whereas Potamotherium appears to be a morphological link between Lutra and Phoca, Semantor seems an equivalent link between Potamotherium and Phoca. Except for size (Semantor was much larger), its femora are identical to those of Potamotherium. Semantor's pes is more similar to that of Phoca than that of Potamotherium (Savage 1957).

Despite its late appearance in the fossil record, Semantor was considered by Orlov (1933) to be a large, lutromorphic pinniped, retaining the ability to move overland. Its foot was wide, and showed a degree of digital elongation parallelling, but less extreme than, that of Enhydra. In the Sarmatian basin, Semantor (though found in a Hipparion bed) was associated with true seals. Orlov concluded that it was "a coastal predator of Neogene rivers, as adept on land as in water." Some investigators, such as Akhundov (1963), believe that Semantor was principally or entirely aquatic - not merely seal-like, but virtually phocid (at least ecologically).

Thenius (1949), working only from Orlov's data, considered 55% of Semantor's traits to be otter-like. Only 6% were phocid-like, and 38.5% were intermediate. The sacral vertebrae in particular are otter-like, as is the complete fusion of the cuneiformia I and II, distinct from all seals (Orlov 1933). Chapskii (1961) considered Semantor a mustelid that resembled seals more closely than does Enhydra. To Akhundov (1963), Semantor "only displays elementary changes in the direction of seals."

Despite Semantor's large body size and general streamlining, the relatively conservative development of its rear phalanges suggests that in terms of adaptation to propulsion, this genus was a little inferior to the later sea otter. The kushta otters today succeed in exploiting the resources of their marine-coastal habitats with even less pedal modification. As the ensuing discussion will illustrate, a highly selective factor operates along

the present North Pacific coasts to favour forms able to utilise feet not only in scrambling ashore, but in securing food and refuge on cliffs and reefs beyond the reach both of modern pinnipeds, and of other terrestrial fissipeds.

Semantor seems hardly less ecologically, than the sea otter of its day. By entering rivers, it shared a trait with modern phocids on the Alaska coast. This, similarly, would not affect the frequency of its contact or competition with other marine mammals.

Kirpichnikov (1955) recovered a humerus (Fig. 3) from the same bed as the original specimen of Semantor. He believed the bone came from the same individual (the type specimen). This rather delicate bone was considered otariid by Akhundov (1963) and others, but Mitchell and Tedford (1973) considered it probably Semantor-like.

Necromites, from the Caspian region of the later Pliocene (Bogachev 1940), may be a relative of Semantor. Akhundov (1963) believed this form was even more highly specialised for aquatic life than Semantor, and that it may have been phocid. But there are features which distinguish it from all other seals. If Necromites is kin to, but later than, Semantor, an increased degree of aquatic adaptation would hardly be surprising. This may represent further progress toward functional phocomorphy on the part of the lineage of Semantor and Potamotherium.

The close resemblance of humeri from the Truckee and Niobrara formations the Oregon endocranium, and other fragments, to

both Potamotherium and Semantor, suggest that a series of fluviatile and lacustrine lutromorphs of common origin became highly modified for aquatic life as early as the dawn of the Pliocene. Orlov (1933) established the family Semantoridae for Semantor alone; Bogachev (1940) referred Necromites to this family.

Semantor today is conventionally classified as a mustelid (e.g. Romer 1966). It is difficult to see that Semantor can be assigned to the Lutrinae, chiefly because of the attachment of lower leg muscles to the pelvis. If it is to be subsumed into the Mustelidae, an independent subfamily, the Semantorinae. may well be required to include this and the two Pliocene American species, and probably Necromites. Potamotherium may also be assignable to this group.

The history of the Semantorinae, thus defined, extends from the late Oligocene to the middle (or late) Pliocene. The group disappeared after the Pliocene, once the phocids had entered the North Pacific (Ray 1976a). Since the first semantorine to approach the American Pacific coastline encountered a twelve-million-year heritage of otariids in a diversity of forms it is unlikely that the large otters became extinct because of competition with phocids, unless there was some overlap of a very specialised foraging mode.

By the earliest Miocene, the transition from lutromorphic mammals to post-lutromorphic otarioid and phocoid lineages was complete. The possible marine fissipede Neotherium was widespread in the eastern Pacific until the late Miocene (Mitchell and Tedford 1973). Necromites evidently had become entirely marine

by the mid-Pliocene. These four lineages had advanced beyond the basic lutromorphic structure to a degree allowing, if not presupposing, a marine existence at the time the Lutrinae proper first appeared in a freshwater environment.

C. Lutra and the Lutrinae

Savage (1957) observed that the fossil record of the Lutrinae is still too poorly known to allow reconstruction of a reasonable phylogeny. The lutrines appeared twelve million years after the earliest certainly identified mustelid.

Lutromorphy may be considered exhibited at its most primitive level, somatically, in the earliest true otters. These exhibit the most general aquatic streamlining without specialisations. A similar level of unspecialised lutromorphy is exhibited by some mustelines (D, below). These mammals were nearly as widespread as the lutrines, but only during a shorter period of time (Scott 1937).

In the late Miocene, pinnipeds were becoming increasingly common, and were more diversified than they are today (Ray 1976a). Probably because the pinnipeds were already in command of the sea, otters appearing after the middle Miocene have shown no tendency toward further aquatic specialisation. The modern Lutra is convergent with early Oligocene forms that could have been progenitors of the pinnipeds, but shows "almost no" adaptations to diving, compared with these pinnipeds (Harrison and Tomlinson 1964).

A similar primitivism is evidenced in the first lutrines. Both Paralutra in Europe and Sthenictis in North America appeared in the middle Miocene, and Sthenictis survived to the end of that epoch (Simpson 1945). The first species of Enhydriodon appear contemporaneously in Mediterranean Europe and western North America (Repenning 1976a). This genus had a long, diversified history, producing several species with wide geographic ranges, including some of the largest of all otters, and (although its name is purely fortuitous) may have produced a "sea otter" of its own, Enhydriodon reevei, in Pleistocene England.

The first species of Aonyx, in the late Miocene of China, were little different from modern species of the same genus (Radinsky 1968). The specialisations already in evidence in the Miocene Aonyx are also found today in other otters of maritime habitats (I.3, below).

The most nearly otter-like of all the lutromorphic mustelines, Brachypsalis, was contemporary with these otters. This "supermink" appeared in the middle Miocene and survived to the middle Pliocene, producing diverse and specialised lines, the relationships of which are still in dispute. Brachypsalis was classified as a lutrine by most investigators (e.g. Scott 1937), until Simpson (1945) referred it to the Mustelinae.

The first trace of Lutra-like animals appeared after Enhydriodon, Sthenictis, and Brachypsalis had become widespread in North America. The late Miocene Mionictis exhibited similarities to, and could have been a progenitor of, Lutra (Radinsky 1968).

Paralutra, contemporary with the Miocene Potamotherium, has features conformable with the type predicted for the ancestor of Lutra (Jong 1972).

Repenning (in Mitchell 1966) suggested that otters evolved along two separate lines, beginning in the middle Miocene. "Fish-otters," with highly developed vibrissal sensory receptors, and "crab-otters," with special forelimb-tactual sensitivity, in addition to reliance upon vibrissal sensitivity, are the types. Radinsky (1968) doubted such a dichotomy, because of evidence that forelimb-sensitive otters arose twice, independently - once in Aonyx and once in Enhydriodon. The "facial-vibrissal" line appeared independently in Potamotherium, the lineage probably including the proto-phocids. Much later, the same complex of features appeared again in the genera Lutra, Lutravus, and Pteronura, not known to be kin to the others.

The facial-vibrissal specialisation can be assumed in the ancestors of the phocids, since their limbs became flippers rather than tactile organs. Flippers are more efficient propellers than limbs, and facilitate the pursuit of fast-swimming prey.

Continued use of the limbs as tactile organs indicates a dependence upon slow-moving, benthic animals concealed in algal forests or rock formations. In this respect, Lutra is closer in its adaptive strategies to the ancestors of the pinnipeds than to such contemporary maritime otters as Enhydra or Aonyx.

The two adaptive strategies have recurred several times. I will call the predominantly facial-vibrissal otters "trichotters." These mammals exhibit behavioural parallels with the seals. The forelimb-sensitive otters I will call "thigmotters;" these are otters whose specialisations have no parallel with other groups of aquatic mammals.

Because vision is impaired underwater Radinsky (1968) believed that highly sensitive vibrissae promoted food-finding in rapidly swimming lutromorphs. The vibrissae of most otters are unusually numerous and stout (Pocock 1914, 1921). Radinsky (1968) believed that otters have a higher ratio of receptor neurons to vibrissae than other mammals. The sensitivity to water movements of these vibrissae is refined by a decrease in the degree of overlap between the separate cortical projection areas related to the vibrissae. Exactly that character is evidenced by the skulls and endocranial casts of trichotters (Radinsky 1968).

The secondary sulci, and the dimples that subdivide the coronal gyrus in the otter brain, appear to separate the projectional surfaces of the different units of vibrissae. Potamotherium shows such an enlarged coronal gyrus, similar to that of Lutra and Pteronura, trichotters all (Radinsky 1968).

In the thigmotter strategy, it is the forelimb cortical projection area of the brain which is more finely differentiated. The secondary sulci, and the dimples between the postcruciate and coronal sulci, demarcate areas devoted to the

cortical projection of individual digits or palmar pads (Radinsky 1968). These animals, such as Aonyx, feed on crustaceans and molluscs which must be felt for in crevices, under rocks, or in turbid water, and must often be pried off the substrate (Simon 1966, Medway 1969).

Only a few modern Aonyx populations are recorded as making a living from the sea (I.3, below). These animals are still oriented more to forest cover for refuge than to water, whether salt or fresh (Banks 1931).

The "thigmotter" trend, predating the evolution of any extant trichotter genus, appeared in the middle Miocene with the European Enhydriodon campanii. Enhydriodon underwent a worldwide radiation before the end of the Miocene, producing five diversely adapted species, but the "thigmotter" trend characterises the genus to a less refined degree than it does the modern Aonyx. In Enhydra, the secondary sulci also divide the gyrus to a lesser extent than in Aonyx (Radinsky 1968). One of the late forms of Enhydriodon - E. reevei - may have been similar to Aonyx (Repenning 1976b, Kurten 1968); it lived on the sea coast.

The most primitive otters must have made facultative use of both vibrissal and palmar sensitivity. I have heard modern Lutra patting the muddy bottom of a turbid cove, probably with its forepaws (III.2, below). Ultimate preference for one foraging mode over the other would be determined by the local preponderance of nektic versus benthic foods. Lutra may be an example of the

positive selection for a retention of primitive generalism.

The history of Enhydriodon exemplifies the problems which arise from the interpretation of food habits in reference to dentition. There is a long hiatus between records of the first and last specimens of Enhydriodon in North America. The latest American species was still anatomically very primitive (Repenning 1976b). It probably observed the same somatic conservatism which Lutra has found adaptively successful today. Enhydriodon disappeared from North American horizons at the beginning of the Pleistocene, shortly before the appearance of the analogous Enhydra (Repenning 1976b).

Enhydriodon may have made its last appearance on the coast of England, as the North Atlantic waters cooled. E. reevei was possibly a cognate of the contemporaneous North Pacific sea otter. The parallels between the two are so close that Kretzoi (1961), among others, flatly calls E. reevei a sea otter. Kurten (1968) referred this form to Aonyx reevei. Aonyx otters, characterised by broad, blunt-cusped teeth in the trend the modern Enhydra carries to an extreme, were still present in Europe from the Astian to the middle Pleistocene.

Kurten doubted whether E. reevei could be specifically distinct from Aonyx bravardi. A. bravardi is not anatomically more specialised than the modern Aonyx. And E. reevei disappeared from Europe at the same time as other Aonyx species.

Repenning (1976b) considered that, for all its aonychoid convergence, E. reevei developed from a Spanish lineage, a form like E. lluecai. There was no apparent genetic link between this form and Enhydra, although Repenning is quoted (in Kurten and Anderson 1980) as ascribing Enhydriodon ancestry to Enhydra.

Repenning ascribed identical habitats to both Enhydra and E. reevei, and agreed with Savage (1957) that "dental characters are less readily moulded to environmental conditions than osteological ones."

The traditional view of the dental analysis of fossils is summarised by Taylor (1914):

> A crushing dentition may characterise the transition from land to water habitat. The more compressed and acutely tuberculated cheek-teeth of land dwellers, to the more nearly isodont teeth of marine forms, where dentition serves the function only of catching and holding; the intermediate, the broad dentition fit only for crushing.

This formula does not correlate with food habits and dentition observed today. There is no reason to project such assumptions into the past.

In Glacier Bay today, summer food preferences for many individuals of Lutra canadensis, and most individuals of Phoca vitulina, are identical. Some degree of exploitation of the same food base is shared by Mustela vison, and the less frequently observed Eumetopias jubatus. While dentition, when highly specialised, can be an index of marine habits, it can not be used, when still generalised, to argue against such status. Food

habits change faster than teeth.

Enhydra today continues the trends, if not the genes, of Enhydriodon. Sea otters locate and dig food from the bottom in turbid water, or in algal forests, through reliance on manual dexterity (Shimek 1977, Shimek and Monk 1977). That both Enhydra and Aonyx have marine or maritime habits today, makes inescapable the conclusion that the potential, at least, for predominantly maritime exploitation, and possibly residence in the sea, has existed for at least fifteen million years for a thigmotter lineage. This strategy guarantees ecological evolutionary continuity to the strictly lutromorphic somatotype.

Both thigmotter lineages had begun a radiation before the end of the Miocene. The earlier trichotters had produced the semantorines, and through another branch, the highly modified phocids.

A new line of trichotters appeared at the beginning of the Pliocene, evidencing that still very generalised vibrissal-sensitive otters had survived. Repenning (1967) assumed an East Asian or Indian origin for Lutra, an assumption which failed of any evidence at the time it was made. The evidence which has since accumulated remains equivocal on the matter, but there is some reason to consider America, in fact, the point of origin.

The Truckee formation of Nevada is uncertainly dated, but it contains bones correlated with those of Clarendonian (early Pliocene) horizons elsewhere (MacDonald 1956). Lutra made

its first American appearance in this Truckee fauna. The Truckee specimen (no specific name was applied) shows dental trends transitional from L. lutra (always considered the more primitive species ((Kurten 1971))) to L. canadensis (MacDonald 1956).

Evidently Lutra licenti has been reported from the Pontian (Pliocene) of China (Kurten and Anderson 1980). This species appears in the early Pleistocene of China as well. Jong (1972) considered its principal characters to be the same as those of L. canadensis. The American species appears in its unquestionable modern form in the middle Pleistocene of eastern North America (Kurten and Anderson 1980). L. lutra is first recorded in Europe only in the late Pleistocene (Kurten 1972).

Another form found in both the late Pliocene and early Pleistocene of North America, without any Eurasian antecedent is Satherium piscinarium (Kurten and Anderson 1980). This species was sufficiently unspecialised to provide a possible ancestor to Lutra as well (Jong 1972).

Some teeth in the Truckee Lutra, such as the M_1, have hardly changed in subsequent time, and so are identical with that of L. canadensis (MacDonald 1956). The extreme generalisations which are evidenced by this variety of forms suggest that all otter species which have adopted the habitus and strategies seen today in L. canadensis are selected for the conservatism of their anatomy and dentition. Given the fact that the earliest record of the genus

Lutra is found in a North American horizon (at least no less than contemporary with the Chinese L. licenti), the possibility of the origin of the genus in North America, and its migration across Beringia in the reverse direction, must be considered. The presence of so many similar, unspecialised forms in North America, rather than Eurasia (after the time of Paralutra) tends to reinforce the probability that the earliest modern otter lineage originated on this continent.

From its earliest appearance, Lutra exhibited a dental trend the reverse of that of the older and more widespread Enhydriodon. Some of the "especially varied" (Kurten 1972) early species of Lutra had much flatter crushing teeth than in any species still extant. Despite the associations of crabs, fish, and molluscs with this and all otter fossils from the earliest fossil records definite maritime habits are not known for any species (Kurten 1968, 1972). The direction of dental evolution is clearly neither predictable, nor necessarily diagnostic of food habits or environmental correlates. For otters, food habits can be deduced with certainty only from coproliths - and the only coproliths definitely known to be of otters have never been sectioned! (Savage 1957)

Even when L. lutra appeared in the late Pleistocene, a contemporary European species, L. simplicidens, had a relatively more primitive dentition - and even more specialised limbs (for aquatic propulsion) (Kurten 1968).

There were other otters in Asia during the early Pliocene - Sivalictis and Vishnuonyx (Simpson 1945) - and the genus Lutravus (Furlong 1932), which occurs sympatrically with Lutra and a late semantorine in the Pliocene of Nevada, but is so distinct from Lutra that Repenning (1967) considered it a distinct immigrant from Asia. Lutravus halli has the diagnostic characters of Paralutra (Jong 1972), so is probably an Asian immigrant.

The late Pliocene-early Pleistocene otter Satherium, widespread across western North America, is larger than L. canadensis and resembles the saro, Pteronura brasiliensis (Kurten and Anderson 1980). Kurten and Anderson stated that the skull, dental, and skeletal characters of Satherium are not so specialised as to bar the genus from the ancestry of American otters especially of Pteronura. The fossils so far discovered are, however, too late in time to represent genuine ancestry. Otters did not enter South America until the very latest Pleistocene (Jong 1972).

Had Lutra in fact come eastward along the Asiatic seaboard, it would have had many opportunities to become habituated to salt water before its arrival in the New World. This is the same coast on which modern Lutra exploits marine forage. But, unlike the first trichotters to breach the sea, these late individuals found the ocean waters already swarming with otariids, sirenians, desmostylians, and semantorines - especially around estuaries.

Even if Lutra was a latecomer to the same habits and habitats already exploited for twenty million years by better-adapted kin, it replaced such animals over vast stretches of coastline throughout the world (I.3, below).

That such trichotters could reappear in the marine habitats utilised by pinnipeds, thigmotters, and semantorines, and become widespread there long after the success (and sometimes extinction) of other species, shows that conservatism is adaptive. There are always opportunities for generalists.

The first recorded species of L. canadensis dates from the Irvingtonian (middle Pleistocene) of eastern North America (Kurten and Anderson 1980). The close similarity to populations of the earlier Truckee fauna in western NOrth America indicate that gene flow between the two populations probably occurred.

In the early Pliocene, otter and lutromorphic musteline species were numerous. By the end of the epoch, otter and otter-like forms were the most numerous of New World mustelids; it was the golden age of otters (Scott 1937). The species then known are all referable to the genera Lutra, Satherium, Aonyx, and Enhydriodon. This was a sharp reduction from the generic diversity of earlier years. The similarities between Lutra and Satherium indicate a possible sympatry between parallel primitivisms.

At the onset of the Pleistocene, as the Pacific waters began to cool, the first true sea otter (Enhydra) appeared on the

coast of Oregon (Leffler 1964). This mammal was already essentially modern in form (Mitchell 1966). In the late Pleistocene, one lineage of sea otters began an episode of gigantism. Enhydra macrodonta (Kilmer 1972) had larger cheek teeth and a longer tooth row than E. lutris; but the species did not persist.

Enhydra lutris spread rapidly around the southern tip of Baja California, around the Pacific rim to the sea of Okhotsk, and to Japan (Kenyon 1969). Two million years ago, a sea otter died in the present Colville delta of the Alaskan Arctic coast (Repenning, unpublished data), during the Anvilian-Beringian transgression, when sea level was higher, and water warmer, than it is today (Hopkins 1967). There are still occasional injections of sea otters into the Arctic Ocean (Bee and Hall 1956, Zimushko et al. 1968). It is possible that in warmer times there was a resident Arctic population of sea otters. River otters sympatric with sea otters over much of their range today (I.3, below), may have been there with them.

When Enhydra populations were still large, river otters were present in association with sea otters on the Pacific coast (Khlebnikov 1861).

Before the North Pole had iced over, the entry of phocids into the North Pacific, the return there of the odobenids the extinction of the desmostylians and the selection of a single surviving sirenian (Hydrodamalis), settled the modern composition of North Pacific marine mammal fauna. The river otter was presumably part of it from the moment the complex assumed its modern character.

Such a conclusion is warranted on the basis of the evidence of virtual genetic continuity, exceeding the usual degrees of parallelism, of Lutra species continuously across North America and Eastern Asia from the Pliocene, and the continuity today of L. canadensis and L. lutra in identical extent.

The first non-mustelid arctoids entered the marine mammal sphere with the freezing of the Arctic Ocean, but they were thalassopagic, rather than thalassotopic, forms. They are oriented toward ice as a substrate, in what amounts to the exploitation of a floating-island habitat. The only other mustelid in the Arctic is the wolverine, which rarely transgresses on sea ice. River otters in northern Europe, and at the delta of the Mackenzie River in Canada survive in this environment (I.3, below), but have not spread out of their limited ranges there. So limited a degree of activity makes it likely that the edge of the ice-pack is a suboptimal strategy for this species.

D. Lutromorphic Mustelines

Contemporary maritime mustelids are indistinguishable, taxonomically, from inland conspecifics. What light can be shed on the history of lutrines by the study of modern mustelids which, to a lesser degree, share their maritime orientation? Evolution being nothing if not competitive, the mustelines did not stop their drive to parity with the lutrines at the failure of Brachypsalis (which, anatomically, was better prepared for maritime existence than is the

modern mink.)

Mustela appeared before the middle Miocene. Martes, also to test the strategy of coastal foraging punctuationally, is first found in Middle Miocene horizons (Kurten 1972).

Three species of Mustela today express the same trends perfected long before by species of Brachypsalis. Mustela putorius, the polecat, seeks food in and along streams. It is not so specialised as the other two, and represents the proto-mink stage (Kurten 1968). The minks proper are of American origin. Mustela vison is active on all maritime coasts of this continent except the Arctic (and points at which inland populations are not found).

The sumpfotter, Mustela lutreola, an offshoot of the mink and a latecomer to Eurasia (Kurten 1968), is smaller than mink (Novikov 1956). But does this mean smaller than the smallest mink? American mink exhibit a wide range of body sizes. The smallest Atlantic coastal mink are half the size of Alaskan mink (Prentiss 1903), yet swim in cold water as did the extinct "sea mink" - itself the same size as modern Alaskan mink (Mansueti 1954). The sumpfotter is not known to occur on marine coasts anywhere (Ognev 1972). The size of the smallest M. vison may represent the minimum threshold of body size permitting adaptation to the exploitation of cold salt water.

Only twenty fossils of mink are known. These date only from the Irvingtonian (middle-late Pleistocene). All occur over approximately the same range as the modern mink. Pleistocene mink did

not differ in size or morphology from extant populations (Kurten and Anderson 1980). Mink customarily hunt from the shore, while otters hunt from the water (Erlinge 1969, 1972). The modern mink has been a marine swimmer and fisher on the New England coast for thousands of years (Waters and Ray 1961). Benthic and sessile marine organisms constitute the primary food base for mink on the shores of Alaska (Harbo 1958, Croxton 1960). Mink have trouble catching any but very small fish (Erlinge 1969).

The study of the sea mink may have a bearing on some of the questions, relevant to otters. which are discussed in this study. For years, a distinction was assumed between inland mink and sea mink, although Prentiss (1903) recognised very early that there were no osteological or dental distinctions between the two forms.

The sea mink - about the size of an Alaskan mink - was twice as large as inland New England specimens (Mansueti 1954, Manville 1966). Specimens of sea mink were known from archaeological middens on the New England coast. The animals were seen and trapped until 1894 (Manville 1943). Since the disappearance of the sea mink, ordinary mink have been observed swimming in sea water over the same coast, and have been trapped from islands too small to support indigenous populations (Mansueti 1954). Trapping was not directed at the sea mink alone, but only the sea mink was exterminated (Hollister 1913).

The pelage of the sea mink was reddish or red-brown. much coarser than, and had a peculiar smell compared to, the smaller

mink. Since both forms were seagoing, this could not have been a response of their common sebum to salt water. The quality of the sea mink's fur was poorer than that of the smaller mink (Hollister 1913). Fur traders at the turn of the century were quoted by Hollister as saying, "We still get mink from this coast which are quite large, and whose fur is coarse - but we get none of the great sea mink of the past."

In size, its habit of eating mussels, and of going up brooks to hunt inland, the sea mink was identical to the common maritime mink of southeastern Alaska. Similar distinctions between the pelage of inland and maritime mink have been described for the mink of British Columbia (Racey and Cowan 1935) and for those around Suisun Bay, San Francisco (Grinnell et al. 1937). All reports associate a coarser, lighter-coloured pelage (called "cotton mink" in California) with salt water habitats. This suggests that the sea mink (which was finally abolished as a separate species, "Mustela macrodon," by Manville, 1966) was only a local expression of a widespread adaptive response of one mink species to local characters of the coastal habitat.

Perhaps selection for the divergence between New England's two types of mink may be illuminated by an observation of my own. Mink were quite abundant in the Pacific coastal area of Glacier Bay where for two years I carried out studies on the ecology of overwintering mammals (II.1. below). The first winter, mink were abundant along the shore, and widespread in inland ranges. Small

mammal populations were high, and shore mink were dependent chiefly upon rodents and spent little time fishing. Most of their fishing was for crabs, which is the minks' predominant food in summer.

In the second winter, when all populations of small mammals, including shrews, fell to extreme lows, the number of mink on the shore increased for a time. Evidence of inland-ranging mink dropped sharply.

After a month of heavy snow, the shore mink population had returned to its original numbers. Inland mink ranges remained vacant. This may be an index of the survival value of the more eurytopic and stable maritime habitat compared to nutritionally restricted inland ranges (Home 1977).

Given the sudden elimination of inland prey species, moderate genetic variations might readily become dominant in a local group insufficiently differentiated at the subspecific or specific level. A mustelid population which survived such a decline by remaining at the maritime frontier would thus be the sole gene pool from which expansion into, and reoccupation of, vacated inland habitats could begin. Only if such a population renewal failed many years in succession would sea mink be likely to exhibit speciation. Given the apparent morphological conservatism of mustelids, and maritime mustelids in particular such changes might be very slow. Four thousand years' accumulation of sea mink specimens has failed to demonstrate any specific differentiation from the smaller mink (Waters and Ray 1961, Manville 1966).

The same factors applicable to maritime otters may have effected selection for the larger body size of sea mink. Such selection combined incidentally or fortuitously with some of the other genetic traits expressed, would become fixed only in isolation.

Harbo (1958) and Croxton (1960) found maritime mink in Alaska at highest density where their ranges correlated with echinoid beds. I have found mink common along shores without such beds. Such mink rely chiefly on crabs, but depend on small mammals during winter, when fish stocks are reduced or less accessible (Home 1977). On an annual basis, the feeding habits of Siberian mink are just the reverse (Stroganov 1962). Mink are distributed along the Pacific coast of North America exploiting marine waters sympatrically with river otters (Hall 1929, Racey and Cowan 1935, Grinnell et al. 1937, Ingles 1965, Cowan and Guiguet 1973).

An extensive literature treats the introduction of mink into areas in Eurasia where the sumpfotter has been exterminated. Such mink were trapped wild in the interior of the United States and Canada. Many mink arrived at, and became settled on, maritime coasts within five to ten years of their inland introductions in Asia (Yanushevich 1966). Although mink remained commoner along rivercourses (Abramov 1966), populations in the Sikhote-Alin National Park, and on Sakhalin Island, attained densities of 1 to 10 mink/km of shoreline (Lavov 1966). This is evidence that adaptation to salt water foraging can be accomplished within the lifetime of a single

individual (as with otters, A, above).

In southeastern Alaska, mink hunt habitually along the ocean's edge but spend little time immersed in salt water In the course of a shore hunt, one mink may dash into the water, swim 15 to 20 m from shore, dive once and swim directly back to shore with a fish (or other prey item) in its mouth. In my observations, mink never spent more than 30 sec immersed in salt water; dives did not exceed 5 sec in duration. Single swims were often not repeated for hours. I have never seen a mink enter salt water where otters were already swimming.

There is overlap between mink and otter range in overland hunting Mink are more dependent upon small mammals in the winter than are otters.

Mink represent an earlier evolutionary stage, which must have transpired in the development of each otter lineage.

E. Summary

The lutromorphic body, adapted to aquatic, and preadapted to marine exploitation, has evolved from arctoid stock in five separate and independent lineages.

In the Oligocene, at least one lutromorph evolved from hemicyonine ursids, and gave rise to a major branch of the pinnipeds, the otariids, with eight distinct subfamilial stocks. Several other such lutromorphs are implied by fossils still unclassified.

Two lutromorphic mustelids, closely kin and possibly identical, were Potamotherium and the proto-phocid. Potamotherium developed in freshwater habitats with some exposure to coastal lagoons. An increasingly aquatically-adapted lineage descended from Potamotherium but retained its trichotter strategy, retaining its limbs intact. This lineage became, anatomically, the most aquatic of all otters, culminating in the Pliocene Semantor. The lutrogene phocids became more fish-like, employing hindlimb propulsion. The ursid-bred otariids remained dependent on forelimb propulsion, and as a result are more agile on solid substrates.

In the mid-Miocene, two more lutromorphs evolved, giving rise to the lineage of the lutrines (which does not include Potamotherium) and of the mustelines (e.g. Brachypsalis). The "thigmotter," or forelimb-tactile, lineages developed independently in two or more stocks: at least those of Aonyx and Enhydriodon. These types have persisted to the present day (at least ecologically), without significant anatomical change.

In the Pliocene, the primitive trichotter lineage was reestablished in the form of Lutra, and some closely related genera, which appear almost simultaneously in Asia and North America. This genus encountered competition from otter species similar to itself and sympatric with it from their common beginning, as well as from the semantorines. A consistently generalised, eurytopic population was selected. There has been no further selection for

increasingly aquatic specialisations, and such species which did evolve exhibiting such specialisations, such as L. simplicidens, have perished.

The late Pliocene was the golden age of otters, though only four genera remained. Brachypsalis, the "supermink," died out at the dawn of this age. The semantorines disappeared before its end.

In the Pleistocene, the distinct "thigmotter" Enhydra appeared in the North Pacific; a parallel form, probably Enhydriodon, existed in the North Atlantic. With the change of climate, Aonyx species disappeared from temperate zones and became confined to the tropics, without undergoing any anatomical changes. Lutra came to inhabit almost all the coastlines of the Holarctic continents by the end of the Pleistocene. This genus had begun to coexist with sea otters, and with new maritime musteline species. A trend toward gigantism in the sea otters proved unsuccessful.

Satherium, a Pleistocene trichotter in North America, gave rise to the largest of inland otters, Pteronura, at the end of the Pleistocene, in South America. The modern Pleistocene Holarctic species of Lutra, L. lutra and L. canadensis, are only slightly modified forms of Pliocene Lutra species.

Lutra on the seacoast today may exploit any one of several biases in its feeding strategies (III.2, below). This thesis will show that one pod is reinforced in a "supermink" strategy, equivalent to that of the precursors of modern otters. Another exhibits a "roensis" strategy, equivalent to that stage

of equal reliance on trichotter and thigmotter specialisations
A third, the "phocoid" strategy, reflects the specialisation which did in time produced the phocid lineage from otter origins. It is this ability to shape habits and strategies to the specifics of any terrain which has made Lutra so successful along the coast of the world-ocean.

Seagoing divergences have occurred repeatedly in mustelid evolution. Sometimes the result has been progressively more specialised marine adaptations, with complete abandonment of terrestrial dependence. When some species have become entirely marine in their life histories, other, less specialised mammals occupy the coastal niches abandoned. Some fissipeds have adapted to such habits without sacrificing their fissiped character - Neotherium, Lutra, Aonyx, M. vison, and others.

Along the Alaskan shore today, mustelid and pinniped foragers specialise in the exploitation of shore zones to a degree directly proportional to their anatomical specialisations. The marten, principally inland and arboreal, is a scavenger and sessile-animal predator in the intertidal zone, but only rarely. Marten descend to beaches to scavenge chiefly when small mammal populations drop to cyclic lows inland.

The mink, swimming in salt water only for brief daily periods, and poor at fishing there, tends to forage along waterline and to select slow-moving foods (echinoids, crabs).

Otters occupy a diversity of habitats and exploit a diversity of niches. Otters may be entirely sea-fishers, joint sea and coastal foragers, or strict inland-river foragers depending upon the opportunities afforded by the territories they occupy. Sea otters have become wholly marine, but still rely on the proximity of rocky cliffs or reefs. Phocids, otariids, and the lost sirenian Hydrodamalis are displaced increasingly from any terrestrial dependence. Some have become completely pelagic, except at reproductive seasons.

I.3. OTTERS IN MARITIME HABITATS: A REVIEW OF WORLD LITERATURE

In addition to the sea otter, six otter species have been documented in saltwater habitats along the coasts of Eurasia, and of North and South America. Lutra sumatrana, L. perspicillata, and Aonyx cinerea are restricted in range to coasts of tropical Asia, as discussed below. Lutra felina, evidently the first Pleistocene invader of South America (Jong 1972), occurs only on the west coast of far southern South America. Lutra lutra ranges over the greatest area and diversity of habitats, from the Arctic coasts to equatorial beaches. Lutra canadensis is a maritime mammal today only on the western coast of North America between California and the Aleutians, although it has evidently inhabited Atlantic coasts in the past (Beston 1929, Manville 1942).

Very little of the literature about L. lutra and L. canadensis even mentions the occurrence of these species in saltwater. Canadian writers (e.g. Seton 1910 and Banfield 1974) indicate that otters were living on the coasts of Quebec and Labrador. There have been sightings, if only a few, on islands such as Anticosti, Prince Edward, Orand, and Manan (Harris 1968). Manville (1942) believed the otters of Mt. Desert Island, Maine, had gone into the sea there formerly, but they were extinct by the time of his study. Beston (1929) recorded a single sighting of an otter in the surf near Cape Cod as if it were an unusual event. Atlantic maritime otters, if they still exist, must be rare.

Until 1937, otters were documented in maritime habitats on the Pacific coast as far south as San Francisco Bay (Grinnell et al. 1937). This may no longer be true. Otters are found almost continuously from the coast of northern California and along the Pacific seaboard to Unimak Island, Alaska.

In Suisun Bay, between Sacramento and San Francisco, Grinnell found otters living in the tule marshes. These otters went so predictably to the beaches to fish in tidepools that trappers there formerly timed their sets with the lowest tides. Grinnell believed that these otters remained in tule marsh ponds at most seasons, travelled along the upper courses of rivers during the summer, and returned to the seashore in time for the fall fish migrations. The otters remained around the salt marshes through the winter, and bred there in the spring.

The type specimen of Lutra canadensis from California was taken from Grizzly Island in Suisun Bay (Goldman 1935). Grinnell's note that entire otter families were usually seen together in the salt marsh area indicates parallels between California pods and those of coastal Alaska. In this respect, maritime pods seem to differ from most of those residing inland. Grinnell also noted some difference in pelage colour of maritime, compared to inland, otters, but considered this only an incidental, or even seasonal, character.

Grinnell indicated that otters were found along streams and in marshes throughout the northern half of California, and near the coast everywhere north of San Francisco. Otter scats

along the coast of Humboldt County were composed almost 100% of the freshwater crayfish, Astacus klamathensis.

I find no records from Oregon. In Washington there are a number of river otters in the sea (Kenyon 1969), although Ingles (1965) reports only those of the San Juan Islands as having "actually taken up a marine existence." Hayward et al. (1975) considered this a recent development. The probability is quite the reverse (below).

Data on the former range of the sea otter suggest that sea otters did not usually occupy protected passageways. Consequently Puget Sound must have been free range for the kushta otter, even when sea otter populations were maximal (Kenyon 1969). The same was also true in the archipelagic channels of British Columbia and southeastern Alaska (Kenyon 1969).

Carl (1966) reported river otters feeding on crabs, fish, and occasional birds and mussels in Victoria Harbour, Vancouver Island, and other shores. Hatler (pers comm.) observed many pods on the west coast of Vancouver Island. and on Vargas, Wickaninnish, Morfee, Arnet. Cleland, and other small islands, utilising all shores, and moving through channels between these islands.

Kennedy (1968), Hayward et al. (1975), Foottit and Butler (1977), and Verbeek and Morgan (1978) all observed otters on or around small islands near the west coast of British Columbia, especially in summer, when these islands were covered by nesting colonies of sea birds. Otters did not necessarily attack birds when both were present on the same islands.

Racey and Cowan (1935) documented river otters resident along the entire seaboard of British Columbia. The majority of this population "breeds in salt water." Individuals ascend rivers only rarely, usually in winter.

Taylor and Gough (1977) saw river otters "in numbers" near the east coasts of the Queen Charlotte Islands, where sea otters have once again been sighted.

LaPerouse (1799) recorded otters at Lituya Bay in southeastern Alaska in 1786. At that time, sea otters were more abundant. In the period of 1817-1832, more river otter pelts were taken from salt water than were pelts of sea otters, in southeastern Alaska (Khlebnikov 1861). Khlebnikov discusses the period in detail, noting that large numbers of river otters were ocean residents; few were taken from rivers or lakes.

Otters fish in the sea around Sitka in the Sitka Narrows, and in Fish Bay (Scheffer 1953). Alaska Department of Fish and Game (1977) traces otter distribution from one end of southeastern Alaska to the other, noting that all bays, fjords, and islands and some open coastline, have resident otters Most otter trapping in this area is conducted along the shore.

The National Park Service has kept wildlife records in Glacier Bay since 1954. An otter pod was resident on the lagoon island in Bartlett Cove when the first structures were built there (1954). Despite massive construction through 1958-59, and again in 1965, these otters did not abandon their island den until 1968. They continue

to fish in the lagoon daily.

Otters were first recorded in Dundas Bay in the 1920's (Dixon 1932). These were trapped there by a resident, Harbison, for twenty years, until 1954. The present otters spend time along the Dundas River as well as in the bay (Home 1973).

In Glacier Bay, the distribution of river otters is nearly uniform along the southern part of the coast. Otters are distributed widely, but less uniformly, around the northern, more recently deglaciated inlets (II.1, below). Otters in Geikie Inlet, on the west coast of Glacier Bay, move along the river to Wood Lake (map, Fig. 5). In Tarr Inlet, otters have been observed in the periglacial waters of Reid and Tidal Inlets. In summer, 1978, three otters were seen near the face of Margerie Glacier, at the uppermost terminus of Tarr Inlet. These otters were only 1 km from the face of the largest tidewater glacier of the area (G. P. Streveler, National Park Service Gustavus, pers. comm.).

Otters have been observed in Muir Inlet: continuously in Goose Cove since 1965; at Rowlee Point since 1967; at the Nunatak river mouth only between 1967 and 1969.

Garforth Island was once criscrossed with otter trails. Otters had been seen there frequently until 1977, but were not seen in 1978. There is an incidental record from Willoughby Island (June, 1965) (Home 1973).

A major part of the present study was conducted on the Pacific coast of Glacier Bay National Monument. One otter pod each maintained residence in Torch Bay, Dixon Harbour, Boussole Bay, and

Palma Bay. Probably there is a pod specific to each of the coastal fjords.

Otters are still found in Lituya Bay. Today they den on Cenotaph Island. These are not descendants of the first otters sighted in 1786, since all resident mammals are removed from this bay every twenty or thirty years by giant seismic waves (Miller 1960). There are pods along the Pacific coast as far north of Lituya Bay as Sea Otter Creek (Home 1973). The pattern is probably consistent northward.

River otters, as well as sea otters, are found in Prince William Sound. Don Calkins (Alaska Department of Fish and Game Anchorage, pers. comm.) finds both species in about equal frequencies in the sea, near Hinchinbrook Island. Calkins doubts whether both occur with the same associations of food fauna and bottom types. Ornithologists have observed otter predation on several bird rookery islands in Prince William Sound (B. Kessel, Department of Biological Sciences, University of Alaska, pers. comm.; P. Mickelson Department of Wildlife and Fisheries, University of Alaska, pers. comm.). The late David Solf (Alaska Department of Fish and Game) studied seagoing river otters in Eshamy Inlet on the west side of Prince William Sound; he was the first to record submarine vocalisations.

Along the southern and southeastern shores of Kenai Peninsula, otters are seen in "quite high" populations (Bailey 1977). On the southwestern tip of the Kenai, these animals feed on Dungeness crabs and several species of fish (Bob Nelson, Alaska Department of Fish and Game, Dutch Harbor, Ak. pers. comm.).

Otters are seen in the sea around Kodiak Island, especially in Uyak Bay, and in the waters between the island and the mainland. Here they are virtually sympatric with sea otters (Clark 1958; Murie 1959). Both Afognak and Nagai Island have resident populations of otters active in the sea (Goldman 1935, Murie 1959). Unimak Island is the westernmost extreme of the seagoing canadensis range in the Pacific (Murie 1959).

Otters are present inland and along the shores of the Alaska peninsula (Osgood 1904). They occur along the western coast of Alaska as far as Unalakleet (Manville and Young 1965). Otters live on offshore islands in the Bering Sea (Solf 1972), but are absent from the Seward Peninsula. There are otters on the coast of Kotzebue Sound, probably having descended the Kobuk and Noatak Rivers. Otters are documented as far north as Kivalina (Manville and Young 1965).

In the interior of Alaska, the south face of the DeLong mountains limits otters' northward range. Although Solf (1972) believed otters could be found as far north as Point Lay on the coast, and inland east of that point, Pruitt et al. (1960) found no sign of them anywhere north of Cape Krusenstern.

Valkenburg and Magoun (1977) documented a slow northward range extension by river otters over the north slope from the Brooks Range. Some animals occurred along rivers flowing into the Arctic Ocean. Porsild (1945) found otters in the Mackenzie delta in the 1920's. Trapping yielded only one or two, or none, per year.

This was not a recent range extension. River otters occurred in the Mackenzie and other rivers to the east, "virtually to the Arctic sea," in the early nineteenth century (Richardson 1829). Sightings which were referred to sea otters by Bee and Hall (1956), in Harrison Bay and other points in the Beaufort Sea, may represent river otters which had reached the coast via the Colville and other rivers. Since otters are not known to Eskimo hunters in this area a mistaken identification could occur.

But sea otters have reached points even farther from the Bering entrance, in Siberia (Zimushko et al. 1968). These Alaskan Arctic records may also be authentic.

The mouth of the Mackenzie is no longer a wilderness, and there is no information on the otter population there today. Reports from other parts of the Canadian Arctic coast (Soper 1944, Doutt 1954, Harper 1956, 1961, Banfield 1974, etc.) make no mention of any otters.

Otters are recorded in South America only from the late Pleistocene (Jong 1972). The species which is considered by Jong to be the earliest invader is found today as a chiefly or entirely maritime population in a habitat nearly identical, in ecological generalities to that of southeastern Alaska. This species, the chungungo, Lutra felina, evidently ranged inland in the past, and is still observed in rivers to as much as 650 m in altitude (Simon 1966). From the many fjords and islands forested with Nothofagus/

Araucaria on the Chilean coast, to the dry, sandy beaches of Peru, the chungungo ranges in rafts of individuals, which evidently are migratory.

Physically, this animal differs little from L. lutra or L. canadensis, except that it is, on the average, the smallest of maritime otters. The average chungungo measures only 1 m in length and weighs from 3 to 5 kg (Martin 1977).

The chungungo's chief food is the prawn, Criphiops caementarius, which is common near Peru. Because of the chungungo's impact on these prawns, the otters are shot by Peruvian fishermen (Simon 1966). This species was hunted with dogs on Tierra del Fuego by Yahgans and Alkalufes (Cabrera and Yepes 1940), with methods strikingly reminiscent of those used to hunt L. canadensis in Prince William Sound, by Chugaches (Solf 1972). The denning and feeding habits of the two species are also similar.

Like the Alaskan kushta otters, chungungos carry their food to rock surfaces to eat. However, since shrimps taken in Alaskan waters are eaten afloat, the same may be true when the chungungo catches prawns. As shown below, a heavy reliance on shrimps is the chief factor removing dependence upon terrestrial substrates in otter populations and is probably the cause of the chungungo's increasingly maritime activity.

This otter also takes an austral cognate of the king crab, Lithodes antartica, which it fishes from "considerable depths"

(Coppinger 1883), and it also takes volutes and cuttlefish (Darwin, in Waterhouse 1838).

The chungungo is the only marine otter showing pelage distinct from that of other otters. There are points of resemblance between this pelage and that of the maritime mink (I.4, below).

Although Darwin (in Waterhouse 1838) found the chungungo everywhere from Tierra del Fuego in the south, to the coast of northern Peru, and saw it commonly on the Chonos and Chiloe Islands, it is extinct today on Tierra del Fuego and around the Straits of Magellan (Cabrera and Yepes 1940). Today L. provocax is more common on the islands around Cape Horn (Harris 1968). Anderson (in Simon 1966) believes that the chungungo "probably evolved from a stream-dwelling species that adapted to a marine environment, after isolation in coastal habitats as a consequence of the progressive aridity in middle latitudes of South America's west coast."

Deglaciation of the Chilean fjords with concomitant expansion of protected saltwater ranges, followed a course parallel to that in southeastern Alaska (Vuilleumier 1971). R. Brownell (pers. comm. to F. H. Fay) believes that the inland populations of the chungungo may only recently have been decimated.

In southern Chile, where the chungungo was most common, the climate and topography resemble the coasts of the Northwest Pacific. The habitats of individual rafts of chungungos seem to be identical with those of Alaskan kushta otters in terms of ecological context, rainfall, hydrology, weather and climate, and associated fauna.

particularly the presence of many other species of marine mammals.

Lutra lutra, the Eurasian cognate of L. canadensis, differs from the American species only in minor points of dentition. L. lutra occurs throughout Eurasia, and is documented as a habitually seagoing mammal in the British Isles along the north coasts of Scandinavia, parts of Arctic Russia, the entire Pacific seaboard of Asia, and the tropical waters of Indonesia and southeastern Asia. This represents the broadest amplitude of habitats for any mammal ordinarily considered terrestrial.

British kushta otters are described in an abundant, but largely anecdotal, literature. Otters are maritime residents along the coasts of Devon and Cornwall (Tregarthen 1929), Wales, western England, especially around the Lake District and on offshore islands (Stephens 1957, Cranbrook 1977). Stephens believed that the majority of these populations alternated between maritime and freshwater habitats, and moved inland in winter.

On the east coast of England, otters have been documented in seagoing habitats near Lindisfarne since 685 A.D. (Waddell 1934).

Migratory habits are not confirmed for any pods on the Scottish coast; these are observed in the same ranges throughout the year (Elmhirst 1938). Some inland otters in England have made treks as far as 81 to 97 km from habitual freshwater bodies to the sea coast (Stephens 1957).

Maritime otters in Devon and Cornwall are said to have low rates of tick infestation (Stephens 1957). Stephens wondered whether inland otters sought sea water as a means of ridding themselves of these ectoparasites. Even if purposefulness in such great journeys were assumed, or it could be accepted that the sea was a conscious goal, I question whether parasites would be lost in such forays. If otters did rid themselves of the outbound load of ticks, and then returned overland by the same routes, reinfestation would occur at about equal rates. The skin of an otter is not wetted during swimming if it is, the resultant chill can be fatal (Stephens 1957· Kenyon 1969). The fur does not take up water, and ticks, being facultatively anaerobic, would probably not be displaced. The low frequency of tick infestations among littoral otters probably reflects the lack of opportunities for reinfestation, because of the low number of refuges for tick attachment, and dormancy between host infestations.

Sea otters are wholly lacking in ectoparasites (Kenyon 1969). Kushta otters may be nearly so, in Alaska.

The greatest density of otter populations in England occurs along small rivers flowing directly into the sea (Cranbrook 1977). In Scotland and Ireland, otters have long been known as common animals on all rocky seacoasts and outlying islands. even where there is no fresh water (Macgillivray 1838. Lydekker 1895, etc.).

As early as 1834, Ogilby proposed the distinct taxon Lutra roensis for the large, dark, seagoing otters of the northern Irish coast. Macgillivray (1838) noted that Scottish otters - called

"sea otters" - were identical to Ogilby's type, but considered this population only a "large and handsome" variety of the common otter. Ogilby pointed out that coastal animals were nearly black in colour, had little of a pale blaze under the throat, and had longer skulls, shorter ears, and flatter tails than inland otters.

These are all aquatic adaptations, showing trends toward those of Enhydra and Pteronura. Ogilby (1834) was "strengthened in his view by the peculiarity of its (the 'new' species) habitation and manners. It is, in fact, to a considerable extent a marine animal, being found chiefly along the coast in the county of Antrim, living in hollows and caverns formed by the scattered masses of the basaltic columns of that coast, and constantly betaking itself to the sea when alarmed or hunted. It feeds chiefly on the salmon, and a premium is paid for its destruction. . ."

In 1920, Hinton confirmed that specimens from the coast still conformed to Ogilby's type in all particulars. But the species designation had no dental or osteological base, and never came into use.

"Sea otter" as a term is applied to otters living in lochs with sea openings (Tetley 1945). Stephens (1957) felt that Scottish maritime otters travelled as much as 50 to 60 km to freshwater lochs to breed, returning to the sea pools to winter, once the inland fish spawning season was over. But after observing otters on the north coast of Scotland for more than thirty years, Elmhirst (1938) concluded, "Otters are extremely conservative in their habits,

and the same places are used in exactly the same way, year after year." These otters did not undertake any particular inland journeys; they hunted and denned around the same middens throughout the year. In one case, the same site was used actively for thirty years, "and according to local traditions, a very much longer time."

Lydekker (1895) believed otters often pursued fish far out to sea, but Elmhirst (1938) found that those of Scotland were principally crustacean feeders. Harvie-Brown and Buckley (1892) felt that otters frequenting the Hebridean shores followed the salmon and sea-trout runs in July. All these records of fish dependence are unsupported by quantitative specifics. Studies with specifics, such as those of Elmhirst, find little evidence for fish.

Harvie-Brown and Buckley examined middens in the rock caves along the coastal basalt blocks occupied by Hebridean otters. Side chambers in these were sometimes littered with discarded food and scats - something inland otters never leave in their dens (Stephens 1957). Maxwell (1960) found such coastal dens clean and packed with bedding, with no food wastes.

Macgillivray (1838) believed maritime otters, especially on the rougher, rocky shores, went inland during winters, or at least during stormy weather. But Elmhirst found otters on the Cumbrae chiefly in the winter. Most pods remained there year-round, and bred near salt water. Elmhirst believed that at least a trickle of fresh water was necessary to any otter's range, but animals on the north coast of Ireland lived on stretches devoid of any fresh water

(Stephens 1957), as are many in the Hebrides and Shetlands (Tetley 1945).

The Shetlands are the islands remotest from the mainland which have been colonised by otters, anywhere in the world. There is a possibility that they were introduced there by human settlers. But they have never been known in the Faeroes, though these islands were settled about the same period (Dorethe Bloch, Forøya Nátturagripásavn, Tórshavn, F.I., pers. comm.).

Populations of seagoing otters in Ireland and Scotland are not distinct from each other; they still interbreed today. Otters have been found to have crossed the 22.7-km-wide strait between the two islands (Macintyre 1950). Otters on the Irish coast are greatly reduced today in numbers (Stephens 1957), probably in response to systematic extermination in the last century. Those remaining are still believed to go upstream in winter (Barrett-Hamilton 1912).

Stephens (1957) listed instances in which otters were caught in crab and lobster pots on the English coasts. Hackett (1873) recorded an otter being found drowned in a lobster pot on the Irish coast. Cox (1947) gave similar instances from Devon.

Otters on the coasts of northern Scotland, the Hebrides, Orkneys, and Shetlands, are not associated with any high growth of vegetative ground cover. Such protective ground cover is obviously not required for otter settlement. This is a parallel with the situation prevailing in Goose Cove Glacier Bay, when first colonised by otters (II.2, below).

Heptner and Naumov (1974) mapped the distribution of Lutra lutra along northern Europe and Asia. The species' range is continuous along the Scandinavian coastline, including the Arctic coast. Otters live on the coast of the Kola peninsula, and in the Barents Sea, and swim to and from the Kil'din Islands through iceberg-dotted channels (Formozov 1927, in Ognev 1972). Formozov believed that fish comprised 93% of the diets of these animals. This may simply be a record of a 93% incidence in scats, rather than as a volumetric component, as fish figures in the reports of Greer (1955). Or, it may be a peculiarity specific to the Arctic resident population.

Otters were once found on the Baltic shore in the Vologda region but this is no longer the case (Bianki 1909, in Ognev 1972). Novikov (1956) found otters still present on the entire Barents coastline, with only tundra between the animals and the taiga many kilometers away.

Otters occupy sites on the entire coast of the Black Sea, the western coast of the Caspian, and the mouths of the Volga and Ural rivers there. Other populations occur along the White Sea coast to the mouth of the Petschera River. East of this river, the overall otter range is defined by tree line as far as the Pacific coast (Heptner and Naumov 1974).

Scattered sightings have been recorded along the courses of the Lena and Kolyma rivers downstream from taiga treeline (but along the courses of these rivers forest extends farther north than at equal latitudes in the surrounding country) (Heptner and Naumov

1974). Otters evidently range farther north only where there is forest cover.

Otters are once again found in maritime habitats on the Pacific coast, south of the Belaya River (the northern limit of the taiga on this coast.) Novikov (1956) recorded otters in seaside locales in Chukotkya and Anadyr, but Heptner and Naumov (1974) do not. For these investigators, Anadirskiy Bay is the northernmost limit of extant otter populations.

Southward from Anadirskiy Bay, otters occur everywhere along the seacoast, around all of Kamchatka, and formerly, but not today, on the Gizhiga coast, the beaches of Shelekhov Bay (Stroganov 1962). Bianki (1909, in Ognev 1972) considered otters more common on the coasts of Sakhalin than on Kamchatka, where most otters were found in lakes and rivers.

The entire Okhotsk seaboard, and that of the Far Eastern Region, seem to be as populous with otters as any part of the Alaskan coast (Novikov 1956). A conifer forest extends along these coasts from Olyutorski Point, around Kamchatka, Sakhalin, and the Okhotsk coast of the Ussuri River.

All these investigators allude to a concurrence between marine otter ranges and exposed rocks or cliffs, especially where freshwater flows cut clefts through which otters move to and from the sea. This is probably true today, since such shorelines are least likely to be impacted by human settlement and activities, and provide the otters with havens from hunting and trapping. It is

arguable whether this is innately the case in an unsettled wilderness. In southeastern Alaska today, it is not.

Heptner and Naumov (1974) considered contemporary otter records from the Kuril Islands questionable. Voronov (1974) found no evidence of otters in the Kurils. Temminck (1847) described the otters of Hokkaido and the Kurils to be larger than other Japanese otters and to have the "finest, richest" fur of them all. He insisted there were no other differences from Lutra lutra. The fur may have been that of sea otters; his specimens were collected in the 1830's.

The entire coast of Japan has been occupied by maritime otters (Heptner and Naumov 1974). Lutra lutra ranges along the coast of China, in reported association with rocky shores, only (Allen 1938). Allen believed these otters fed entirely on fish, but again without quantitative documentation. Swinhoe (1870) found the same species all along the south China seacoast. Otters were especially common between Canton and Hainan, and on the island. Swinhoe also considered these populations predominant fish-eaters.

The coast of Vietnam, the coast and adjacent islands of Thailand, Malaya, and Sumatra, as far as the east tip of Java, are all occupied by seagoing L. lutra (Medway 1969, Heptner and Naumov 1974). The species occurs along the coasts of Burma and Ceylon (Medway 1969), where it overlaps the ranges of other seagoing lutrines (below). Such sympatry of close related species in the same aquatic habitats parallels that of fossil environments in North America (I.2. above).

Maritime otters today inhabit only the northwestern coast of Ceylon, which is also the only range remaining to the island's dugongs (J. Kabeerawaya, Sri Lanka Wildlife Board, Colombo, pers. comm.).

Lutra sumatrana, the hairy-nosed otter, is found in the sea near Penang, Singapore and the coasts of Indonesia and Malaya (Medway 1969), and swimming in the sea near Pangkor Island, in the Malacca Straits (Harrison and Hendrickson 1961). L. perspicillata, the smooth otter, lives around estuaries and on offshore islands, and is seagoing in Malaya, India. southwest China. and Sumatra (Medway 1969), "taking readily to the sea, at least on the west coast of Malaya, and swimming to Pangkor," only a few km from the coast (Harrison and Hendrickson 1961).

Aonyx is the only surviving otter genus, other than Enhydra, which is a forelimb-sensitive species documented as a maritime coastal dweller. Aonyx cinerea, the false small-clawed or true clawless otter, little changed anatomically from the late Miocene Aonyx aonychoides (Radinsky 1968), occupies the seaside in Burma, Hainan, and small coastal islands, and the larger islands of Indonesia (Allen 1938; Medway 1969). Banks (1931) found pods of five or six otters, as well as solitary animals, nosing around in the surf and along shore in many parts of Borneo. These ran into the jungle, rather than the water, when disturbed. Other reports indicate that these otters occur along beaches in large groups (Simon 1966).

The inland forms of Lutra and other genera which range across Asia and Europe are only mildly differentiated (Harris 1968). Only the single species Lutra lutra, without differentiations, encircles all the others along the seaboard from the Arctic to the tropics. This may indicate that otter populations spread much more rapidly (and with less regard for the character of adjacent terrain) along coastlines than along rivers or other features. The variation in the level of vegetational cover, the nature of retreats and feeding sites, and the competition of other species both on land and in the sea, is enormous throughout the maritime range of Lutra lutra.

I.4. THE SPECIAL CHARACTER OF PELAGE IN MARITIME MUSTELIDS

Differences between the pelage of maritime and inland mink have been found on both the Atlantic and Pacific coasts of North America. The sea mink of New England, the "cotton mink" of California, and the maritime mink of British Columbia, are all lighter in colour, and have coarser hair, than the more numerous mink of inland populations (Manville 1966, Grinnell et al. 1937, Racey and Cowan 1935).

The sea otter's pelt is not coarser, but rather much finer, than the river otter's (Kenyon 1969). Colour differences between land otters and kushta otters in North America are not documented. North of Scotland, however, a marine population of L. lutra has been distinguished for almost three centuries by its pale pelage.

Ogilby (1834) maintained that the maritime otters he wished to distinguish as Lutra roensis were darker, generally, than inland animals. Tetley (1945) found considerable colour variation among these "sea otters," but acknowledged that for the majority, the huge was darker than that of inland specimens. Kits were the lightest in colour, and adult males the darkest. Tetley suggested that the colour of the kits approximated that of inland otters, and that the darker pelage was acquired individually during life in oceanic waters.

Especially among the females, many of his specimens had lighter-coloured underparts.

Light-coloured and albino otters have been sighted in the seas north of Ireland and Scotland, especially around the Hebridean islands of Mull, Islay, and Jura, where there is a resident population of white- or cream-coloured otters - "the coat is like a polar bear" (Fletcher 1956, Anonymous 1862, Harris 1968). There is a century of documentation of the continuous residence of this white population, and on the evidence cited in Harris (1968) the light strain has been present continuously for three centuries or longer.

These animals are conspicuously visible even under water (Anonymous 1862), but the majority of Hebridean and Shetland otters, living most of their lives in the sea, are as adults, very dark. Harrison Matthews (1952) doubted whether enough Scottish and Irish specimens had ever been examined to warrant any conclusions about colour frequency.

There is no information as to whether hair texture differs between these Hebridean whites and inland otters. Colour variation is greater among inland animals (Harris 1968).

The Hebridean white strain includes not only pale-coloured animals, but males which are grizzled more extensively than are inland males (Harris 1968). Obviously there is no selection against such conspicuous animals. The only comparable instance in the Pacific is that of the rare occurrence of much-grizzled, almost white sea

otters called "king-of-the-sea-beaver" by Aleuts (Ognev 1972). No textural differentiation between these and other sea otter pelts has been recorded.

The whitening, or consistent paling, of hair in carnivores contributes to a decrease in heat loss, as air fills the cavities of the hair shaft formerly occupied by the pigment (Novikov 1956). Given the rarity of white otters and sea otters it is difficult to assume that the difference in thermoregulation between these and darker animals has any adaptive significance. The chungungo has pale-tipped guard hairs which are semi-erect and harsh to the touch, over uniformly dark underfur (Martin 1977). In this there is obviously no reference to thermoregulation.

In Alaska, I have only two records of light-coloured otters from among all my personal sightings, all reports transmitted to me, and my examinations of pelts at the annual fur auctions in Juneau over a decade. In all of these, I have observed only minimal variation in the dark sable which predominates.

A blond female otter, accompanied by two dark kits was observed resident in Goose Cove in summer, 1975. The resident females of both the previous and subsequent summers were dark individuals (NPS ranger Nigro's log).

In summer, 1979, an albino otter was often seen well out in Soapstone Cove, Yakobi Island, by fishermen; it often approached working boats. This animal was almost fully grown (Sandy Pocsic, Elfin Cove, Ak., pers. comm.). It had not been seen

the previous year.

I have seen no change in the colour of kits as they age: all kits in my observation when first sighted were as dark as their parents.

The grizzling of the muzzle of male otters, by contrast, is almost universal among kushta otters, and is described for those of other areas. All males I have observed were characterised by grizzled muzzles. Informal reports from acquaintances who have made kayak trips around Admiralty and Chichagof Islands, and who often sighted otters, indicate a frequency of grizzled to non-grizzled muzzles in adults equal to the sexual ratio. At present, I allow that any adult otter sighted in its permanent territory can be sexed on the basis of muzzle grizzling. More extensive data are needed to determine whether this may be diagnostic, and from what age.

Otters are said to be difficult to age by such indices as teeth (Stephens 1957), but the males, like other arctoids, can be aged by bacula (Savage 1957). Comparison of the pelts and bacula of trapped and hunted otters may provide a correlation between age and the onset of grizzling. Given the uniformity of reports, such grizzling may be coincident with the assumption of a regular territory, or of regular breeding.

Tarasoff (1974) compared the pelt characteristics of river otters, sea otters, and harp seals (Phoca groenlandica), but his river otter specimens were inland animals from Quebec and Maine. Whether or not maritime, Quebec and Maine otters are the smallest of the species (Jong 1972). Tarasoff found that the river otter's

skin was much thinner than the sea otter's. The M. cutaneus trunci, which governs skin flexion and shivering, is in the river otter generalised and reacts as a whole (to fluff fur on land, and aerate the insulative underfur), while in the sea otter, the same muscle is divided into specialised regions, which contract dorsolaterally.

The fur of the sea otter has twice the number of hairs per unit of skin as a river otter, and four times that of mink. The hair on a river otter's back is as dense as that of Callorhinus ursinus. Although Tarasoff identified three characteristic differences between river otter and sea otter hair as possibly indicative of a gradient of adaptations to positive buoyancy and the uniform temperature of the marine habitat, he used only inland specimens. The differences were: (1) a reduction in the number of guard hairs from the river otter to the sea otter; (2) a reduction in the size and length of the medullae of each hair. the dimensions being larger in the river otter than in the sea otter; and (3) a lateral expansion of the shaft of the guard hairs, 3x that of the base in river otters, and only 2x in the sea otter.

In common with other marine mammals, otters have well-developed sebaceous glands. In the sea otter, the secretions of these glands are spread by continuous grooming· they thereby waterproof the fur. The sea otter's existence depends upon perpetual grooming (Repenning 1976), an activity which occupies 36% of the time of California individuals (Shimek and Monk 1977).

As Tarasoff acknowledged, there is little grooming among any river otters, kushta or inland. Elmhirst (1938) believed that otters had to have a freshwater source with which to remove salt from their fur after coming ashore. None of the otters in my observation have undergone grooming, or made any effort to clean its fur using fresh water, though an ample supply of still or flowing water was available to almost all of them.

There is no Alaskan evidence for the statement that otters emerging from salt water roll or rub their fur dry on vegetation (Seton 1910, Stephens 1957, etc.). Sites so used, "rubs" are not observed on the Alaskan coast.

An Alaskan kushta otter emerging from salt water immediately shakes the entire length of its body and tail vigorously. There is no further attempt to dry the fur, regardless of light level, temperature, or other factors. After emergence, otters are equally likely to remain in open air or go to their dens.

Liers (1951) gave no evidence that the otters he observed throughout their lives groomed frequently. Grooming is rare in all otters (Tarasoff 1974). Evidently the fact that kushta otter fur dries periodically through any 24-hr cycle has a bearing on the lack of a need for grooming. Such drying may compensate for grooming in effect. But in southeastern Alaska otters must often go many days without any opportunities for real drying of fur.

This is a factor which should be studied, as should the special characteristics of the fur of kushta otters, as opposed to inland otters, and sea otters.

II. HABITAT TYPES AND POD RANGES IN THE GLACIER BAY RESERVE

II.1. HABITAT TYPES OF THE STUDY AREAS

A. Methods

The information herein was derived by the methods employed in the studies described in I.1.B, above.

B. General

The types of habitat within Glacier Bay National Monument are not only diverse, but almost continually in flux, because of glacial advance and retreat, tectonic movements, eustatic sea level changes, isostatic depression and rebound, flash floods caused by the breaking of ice dams (jötulhlaupir) with emptying of the lakes previously confined behind them (Derksen 1975), and seismic waves - earthquake-generated rock slides or ice falls into fjords which raise waves to heights of 550 m along the cliffs of Lituya Bay at intervals of thirty to forty years (Miller 1960).

None of these factors functions in complete isolation from, or in total dependence upon, the others. The process of dating even a single event, such as a glacial retreat, is, as a result, complex and tentative. The glacial history of southeastern Alaska

is in broad outline consistent throughout the area (Harris et al. 1974), but it has been studied most intensively in the Glacier Bay area; hence, more details are known in regard to glacial advances and retreats, and the concomitant forest and faunal successions, than for any other area in southeastern Alaska.

Because of the complex of factors listed above, no study of the flora and fauna in any area of the present national park reserve, however exact and detailed it may have been at the time it was conducted, can be extrapolated to other sites or times. This is true even of areas which appear to differ very little ecologically from those areas for which detailed information is available. Factors not taken into account at the time of one study may be significant influences on species composition and individual life history to a degree overriding those factors which were accounted for.

The rain forest which covers the surface of southeastern Alaska today was established during the Pliocene. It both antedated and survived the Pleistocene glaciations (Waring and Franklin 1979). The vegetation and phytosociology of the region have thus changed less than any of the other ecological factors - less than weather, fauna, or the landforms themselves. The Wisconsin ice advance ended over most of southeastern Alaska 15,000 years ago, but massive glacial advances until as recently as 1800 A.D. maintained the regimen of the Ice Age throughout the intervening millennia (Derksen 1975). Massive icecaps and glaciers in the Glacier

Bay reserve continue to fluctuate, and to discharge enormous amounts of ice into the sea on a daily basis.

The Brady Icecap, 2000 km^2 in area, is the source of eight major glaciers which flow east, south, and west from the north-south axis of the icecap itself, on and around the western peninsula of Glacier Bay National Monument. Almost all of these glaciers reach tidewater, and thereby isolate many segments of the coast from each other, by ice and salt water. Such areas are part of the geological mainland, but form biogeographic islands.

Fjords cut by these glaciers during earlier advances distinguish the Pacific coast to Glacier Bay (map, Fig. 5). Much of the fluviatile influx into these fjords today originates as glacial melt, and the silt is transported to the sea bottom of the fjords. Such fjords become more and more shallow annually.

Two of these fjords and valleys, (1) the Dixon Harbor fjord, a narrow, V-shaped valley fed by a glacial outwash stream, and (2) the Boussole Valley, a broad, U-shaped valley between sheer cliffs, were the subject of an intensive ecological investigation conducted by the National Park Service between 1973 and 1975 (Streveler and Worley 1975, 1977). My part in this study, an investigation of the ecology of overwintering mammals and birds (Home 1977), is the basis of part of the present thesis.

These two valleys were flooded by sea level transgression between 13,000 and 11,000 years ago. Their subsequent emergence may have been due as much to tectonic factors as to eustatic

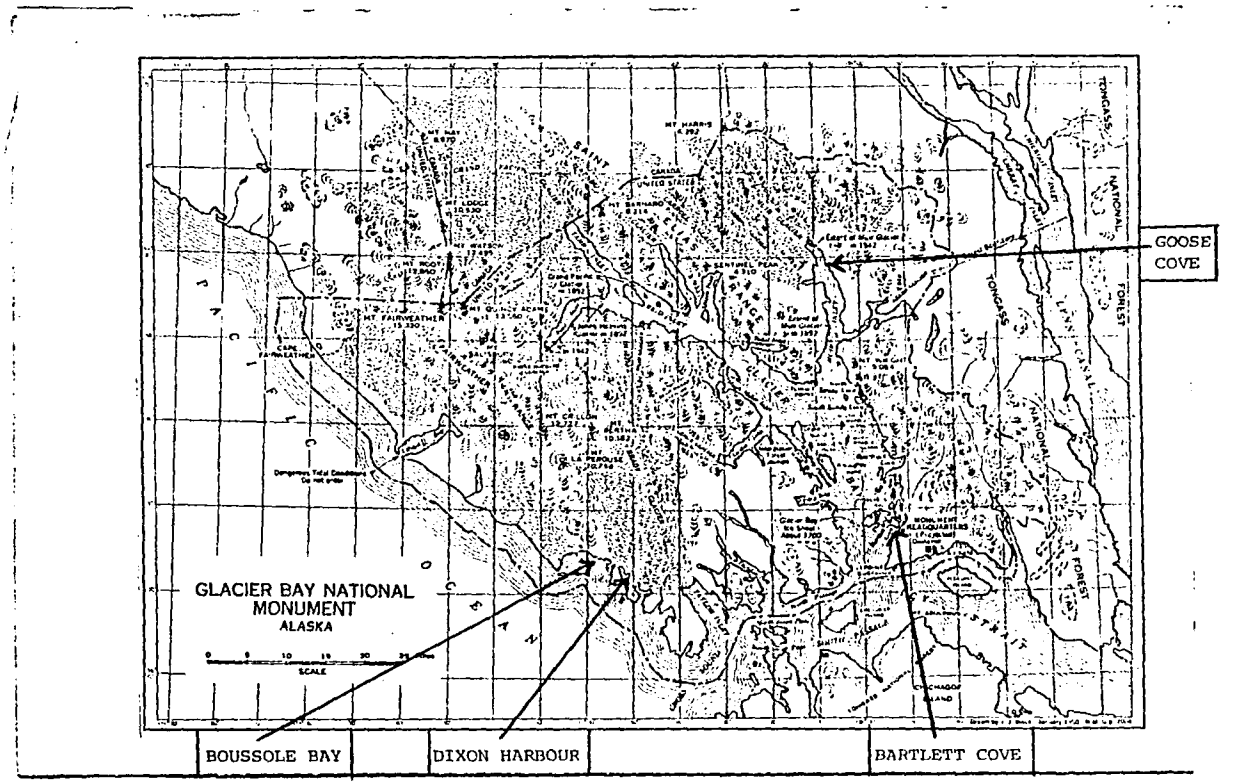


FIG. 5. GLACIER BAY NATIONAL MONUMENT

sea level changes. The Fairweather fault, one of the most active seismic zones along the Alaskan coast, parallels the coastline of these valleys about 10 km west of the present shore. This fault trends inland at Icy Point, only 12 km north of Boussole Valley, and extends northward in a montane valley structure, the Valley of Desolation. Earth shocks are a regular event along the coast, occurring, on the average, once a month. Parts of this coast have been elevated as much as 15 m in a single shock (Miller 1960).

Despite some minor glacial advances through these valleys between 11,000 and 1,740 years ago, the valley floors were above sea level most of that time, probably covered with a vegetation identical with that of the present. Between 1,740 and 1,440 years ago, both valleys were again glaciated. The Dixon Valley glacier extended to the present mouth of the Dixon River. The Boussole Valley was only partly glaciated, and was filled with morainal gravels to depths of 30 m. These deposits were transformed by a river larger than the present one, which discharged volumes of glacial silt. The present river rises from a lake in the northwest part of the valley and discharges no silt into the bay (Derksen 1975, 1977).

These glaciers receded from the valley floors 1,440 years ago, and did not advance again during the Little Ice Age (1650-1800 A.D.), when Glacier Bay itself was completely filled with ice.

Though the Little Ice Age as a phenomenon affected all of southeastern Alaska, a greater volume of ice moved in Glacier Bay than anywhere else in the region (Harris et al. 1974). This glacial maximum reached a peak around 1750 A.D. (Derksen 1975). Since there were otters in or near Lituya Bay in 1786 (LaPerouse 1799), otter populations existed along the Pacific coast while the rest of Glacier Bay was full of valley ice.

Radiocarbon and tree-ring dates from interstadial stumps in Bartlett Cove, at the southern end of Glacier Bay, indicate that these trees were overriden by ice between 1650-1660 A.D. (R. Ackerman, NPS, Juneau, pers. comm.). A Tlinkit city, Tlemshawshiki, was located on the Beardslee Islands at that time, and its destruction by this advance is detailed and dated in Tlinkit oral tradition (Black 1956). Other Tlinkit sites in northern parts of the bay were relocated after the ice retreated on the basis of landmarks of clan ownership (Black 1956). This continuity of human occupation has implications for similar reestablishment, by other mammalian species, within recovered ranges.

The history of the shores and water of Glacier Bay parallels, in outline, that of the Pacific coast. Remains of older forests, chronologically correlated with the vegetational stades of the Pacific coast, have been identified in the northern inlets of Glacier Bay. There is evidence that some forested refugia remained on the cliffs and ridges above the main ice flow (Good 1966).

Dundas Bay, between Glacier Bay and the outer Pacific coast, has not been glaciated in the past 11,000 years (Streveler and Paige 1971), and provided a refugium for forest vegetation and fauna which has since recolonised both the Pacific coastline and Glacier Bay. The present-day forest in Dundas Bay is distinct from that anywhere else in the reserve, containing yellow cedar (Chamaecyparis nootkatensis) and species of herbs and forbs not found elsewhere at this latitude.

Vancouver (1798) found the ice front of this "Tlemshawshikian" advance at the mouth of the present-day Glacier Bay in 1794. Its retreat began shortly afterward (Derksen 1977). Bartlett Cove (map, Fig. 6) had begun to reforest by 1820. By 1882, when Dick Willoughby established a trading post at the Tlinkit settlement on the old site of Tlemshawshiki, salmon were running in large numbers in the Bartlett River, and a cannery was established there (Scidmore 1885).

In 1889, John Muir (1915) charted the face of Muir Glacier, then even with Muir Point. This face was then 97 km north of its 1794 position, and was 5 km wide. In 1899, the glacier's face was shattered by an earthquake. Volumes of ice were discharged into the lower bay; tourist ships were impeded from reaching the face of the glacier again until 1905. No more salmon ran the Bartlett River, and the Bartlett Bay settlement was abandoned (Black 1956; Streveler and Paige 1971).

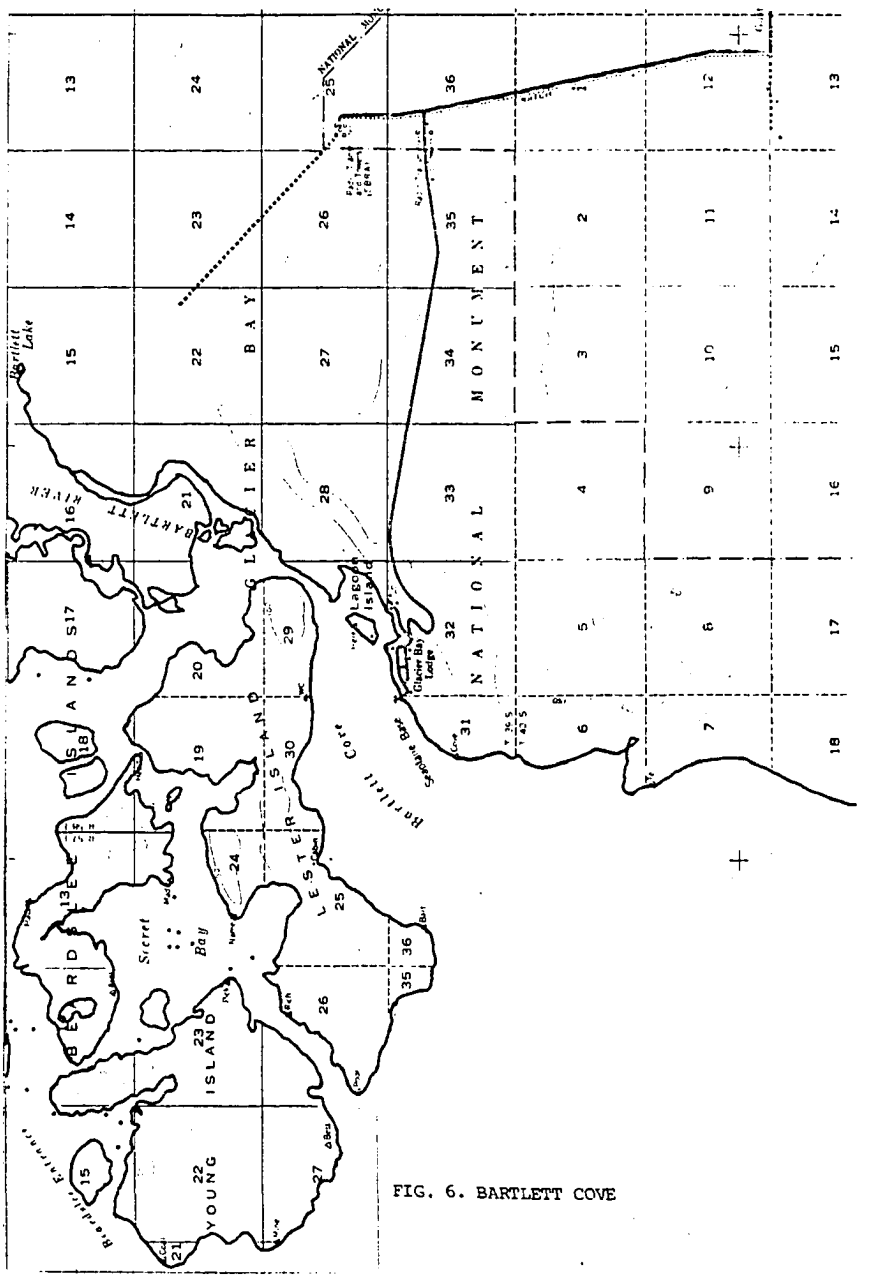


FIG. 6. BARTLETT COVE

In 1925, Goose Cove (Fig. 7), the most recently deglaciated of the study sites in this thesis, began to emerge from beneath the sole of Muir Glacier. It was ice-free within two years (Lawrence 1958).

During the 1890's, geological and glaciological mapping expeditions entered and charted such parts of Glacier Bay was were accessible (Streveler and Paige 1971). Studies of the postglacial revegetation were begun by Lawrence (1958) in 1923, and are now in their fifth decade. Although there were incidental accounts of the mammal fauna in the Bay from the 1889-1892 observations of Muir (1915), only anecdotal reports of mammal activities were made over wide intervals. Examples are those of Bailey (1921), Dixon (1932), and Cahalane (1954).

In 1964-65, Good (1966) conducted the first systematic study of the mammal distribution on the east shore of Glacier Bay and the east side of Muir Inlet. Good assigned each of the small mammal species he observed to a specific zone of vegetation in the postglacial succession. His strict stadial assignments have not been borne out by more recent studies (Home 1973).

As the result of the compilation of a large number of independent studies, and individual field reports. a firm knowledge of the incidence and habits of most mammal species in any part of Glacier Bay is only now developing. Such information can not be extrapolated into conditions of the past.

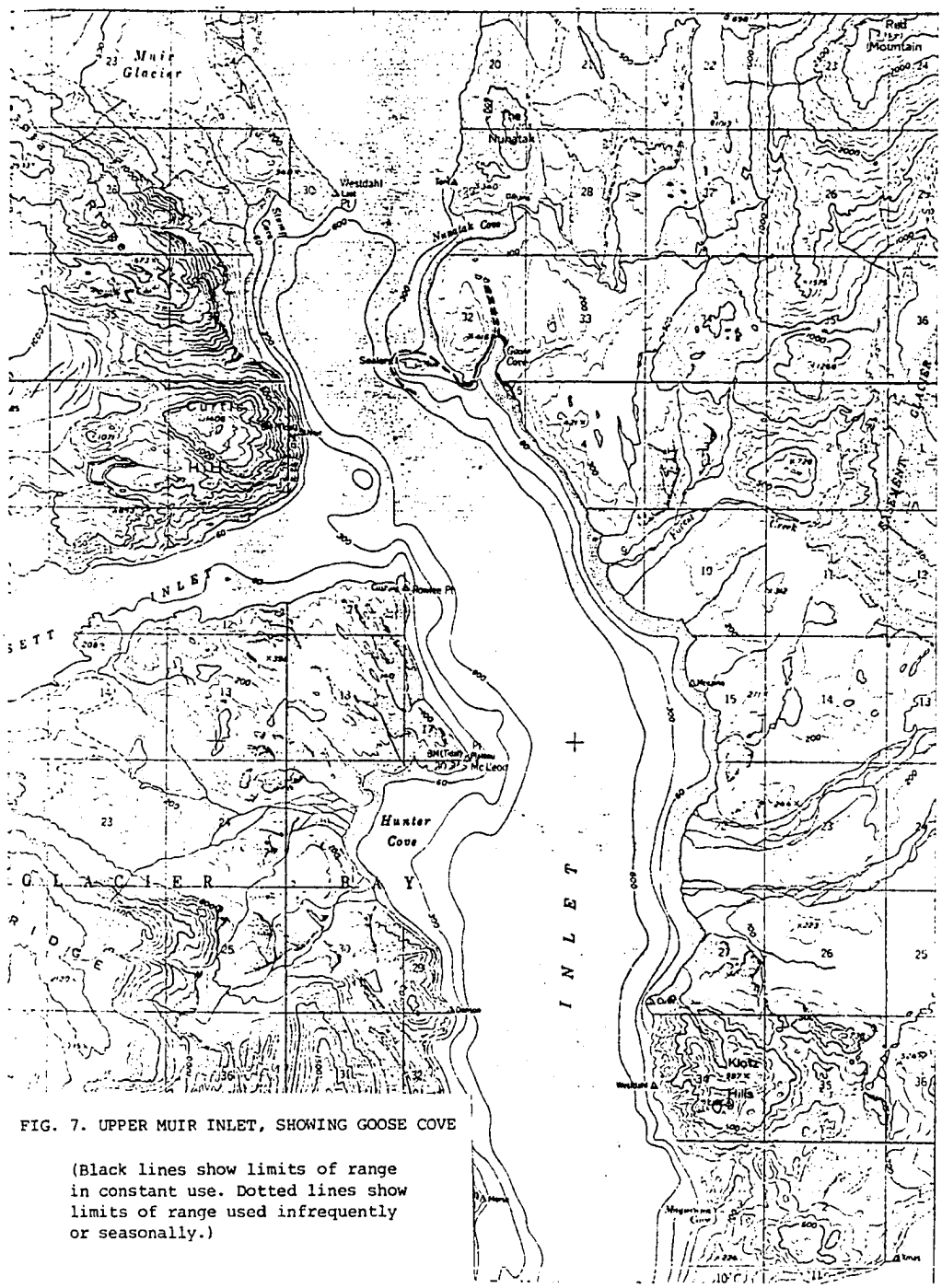


FIG. 7. UPPER MUIR INLET, SHOWING GOOSE COVE

(Black lines show limits of range in constant use. Dotted lines show limits of range used infrequently or seasonally.)

In the process of deglaciation, the shores and bottoms of Glacier Bay have been elevated by isostatic rebound. Very shallow bottoms develop into reefs, islands, and finally supratidal meadows, within a matter of years. Between 1969 and 1974, the rate of uplift around Bartlett Cove slowed from 4 cm/yr to 1.75 cm/yr (Derksen 1977). Succession on this new land area may not differ from that following deglaciation.

The colonisation of vegetation in deglaciated areas follows a similar pattern everywhere in southeastern Alaska. The first plant to appear on postglacial rock or gravel is the mat-forming Dryas. Mats of this species may coalesce into a complete ground cover within twenty years after ice retreat. Red alder (Alnus rubra) may begin to grow in as little as ten years after ice retreat, if the Dryas has, by that time, provided a film of soil. Alder provides a supply of ambient nitrogen in the new soil; this prepares the ground for the settlement of a larger number of plant species. Alder is the main contributor to the change of soil from an alkaline to a slightly acid pH, and is, as a result, replaced by cottonwood, willows, and early spruces (Harris et al. 1974, Meehan 1974). The rich soil these plants colonise becomes depleted in nitrogen, carbon, and protein. The system's carrying capacity for all these intermediate-age species declines as the forest approaches climax. There is a decrease in both the quality and quantity of the food produced (Meehan 1974).

There is also a loss of energy in the transition from spruce (Picea) to hemlock (Tsuga) because of the reduction in ground cover. Spruce forests are depauperate in species, and hemlock forests even more so (Neiland 1971). In spruce forests, the largest amount of bird, mammal, and amphibian activity is concentrated at the fringe of the forest, along waterways and seacoasts.

After 180 years of revegetation, the area around Bartlett Cove today is covered by mature stands of Sitka spruce, interspersed with hemlock. Occasional cottonwoods linger in the forest; those which have survived attain the size of mature spruces.

At Goose Cove, 50 years of revegetation has resulted in a heavy stand of red alder. Some willows and cottonwoods occur along the fringes of alder thickets; these newer species are less than 20 years in place. Occasional spruce seedlings crop up everywhere in deglaciated areas, even on newly exposed ground, but none take hold until the cottonwoods have become established. The nearest permanent spruce are 6.75 km south of Goose Cove.

The largest individual spruces seen anywhere in Glacier Bay are those at the north end of the Boussole Valley, and may be 750 years old (Waring and Franklin 1979). The spruce-hemlock kforest of this and the other coastal valleys differ from the younger forest of Bartlett Cove only in the frequent incidence of mountain hemlock (Tsuga mertensiana).

Since snow cover in these forests is removed repeatedly throughout the winter by rainfall, especially on the Pacific coast, the appearance of these forests on a sunny December day is similar to that of midsummer. Seventy percent of annual photosynthesis occurs in fall, winter, and spring (Waring and Franklin 1979). Mosses, clubmosses, and ferns remain green all year, even under snow, as do such angiosperms as bunchberries (Cornus) and wintergreens (Pyrola spp.). The basidiomycetes, widespread in autumn, are decomposed in winter. Flowering and foliation begin in mid-April, and leaf cover extends until the frosts of late September.

Because of the influence of the Japanese current, which passes the Pacific coast, this coast is much warmer than any other part of the Glacier Bay reserve through the winter. Even bears wake and walk during midwinter warmings.

More precipitation falls as rain than as snow as in the Pacific coast. The annual precipitation totals 280 cm, most of it in fall and winter (Derksen 1975; Home 1977). Some autumnal or winter rains may fall at rates of 7.5 cm/dy for 3 dy in succession. At such times, runoff water in an almost unbroken sheet spills down all rock cliffs and forest slopes into the sea. The resulting lens of fresh water over the saltwater may be as much as 4 m deep (H. Feder, Institute of Marine Sciences, University of Alaska, pers. comm.).

All intertidal organisms in this area are of course euryhaline, since such animals are immersed in freshwater during low tides. Even during periods of little rainfall in winter, snow melt provides almost continual run-off. Subnivean temperatures in southeastern Alaska average only 5^{o} to 6^{o} C below ambient air temperatures. Often, the surface temperature is above 0^{o} C, and a steady flow of fresh water is produced from the continuous melting of both overlying and subnivean snow layers.

On the Pacific coast, precipitation often falls as snow on elevations above 300 m, but changes to rain as it falls below that level.

The greatest snowfall in any 24-hr period on this coast amounted to 11.25 cm (Home 1977).

In winter, air temperatures remain mild. The average day's fluctuation in temperature may be no more than from -10^{o} C to 0^{o} C. Prevailing southeast winds sometimes reinforce temperature drops to produce a chill factor of as much as -43^{o} C, but this is found only as a midwinter extreme, and lasts no more than seven or eight days a year.

Coastal ground fog is rare in winter, spring, or autumn, but is frequent in summer. Southeastern Alaska as a region is characterised by a cover of low, brooding cloud masses at any season of the year. But the winter sky is more likely to be clear on the Pacific coast than inside Glacier Bay.

Precipitation and temperature patterns in the environments of large glacial masses differ from other areas. Such vast volumes of ice modify the weather in their immediate vicinity. Summer rainfall is less frequent in the upper inlets of Glacier Bay, than around Bartlett Cove.

The tidal flux raises and lowers the sea level an average of 5.6 m every 6 hr. Solstitial tides flow up to 8 m over mean low water line. Marine water temperatures vary little from winter to summer (Table 2 compares water temperatures of the study sites). Water temperatures at the faces of the tidewater glaciers, taken daily in the summer by NPS personnel, rarely exceed 3^{o} C.

According to local fishermen and other observers, the mean marine temperatures in the Pacific may fluctuate as much as 5^{o} to 6^{o} C in the same area, from one year to the next. There is no specific documentation for this.

The invertebrate fauna in the intertidal and subtidal zones of the Pacific coast resembles that of similarly silted glacial fjords elsewhere on the coast of the Gulf of Alaska (Mueller et al. 1977). It differs only in that the ten species of starfish found in the Dixon Harbour area represent the highest species diversity of asteroids known anywhere on the Alaskan coast (Duggins and Quinn 1975).

The invertebrate fauna has the "fugitive species" character, in which large numbers of active, widely-dispersing offspring are produced in response to environmental unpredictability

TABLE 1. TERRAIN IN SOUTHEASTERN ALASKA RELATIVE TO OTTER INCIDENCE (from Neiland 1971)

Type of terrain	Percentage of the total area of southeastern Alaska	Otter activity
Rock, snow, icefields Alpine meadow	36.2%	Only at seashore rock and ice faces. None where not adjacent to shores or watercourses.
Muskegs	14.0%	Little and infrequent, adjacent to watercourses.
Wet organic soils	24.0%	Considerable otter activity if adjacent to watercourses, or to the terrain below ↓
Conifer forest, alder brush, grasslands	39.8%	Almost all otter activity is observed along shores and watercourses adjacent to this vegetational complex, and over the surface of such zones. Activity is limited to elevations below 140 m.

TABLE 2. CHARACTERISTICS OF HABITAT OF

Pod name	Coast type
Boussole	Open Pacific coast Forested U-shaped valley with sheer rock walls
Thistle	Open Pacific coast Forested V-shaped valley with steep slopes *Sheltered silty cove
Barco	Sheltered coast of Glacier Bay Forested island and tidal channel system, reefs, islands. Morainal hill and plain margin.
Goose	Sheltered coast of glacial fjord

THE FOUR STUDY PODS (Key to symbols on page 107)

Beach type	Glacial history
Sandy beach 800 m broad, 1.4 km long, bounded by talus, rock cliffs, and rock domes	Unglaciated since about 540 A.D.
+Gravel beaches Rock faces and talus Sandy beaches Mud flats	Unglaciated since about 540 A.D.
+Gravel beaches Scattered boulders Mud flats (not used)	Unglaciated since 1800 A.D.
+Sheer rock face, talus +Sheer-sided granitic dome island Gravel beaches	Unglaciated since 1927 A.D.

(Continued

TABLE 2. (Continued)

Pod name	Freshwater features
Boussole	*Lacogene river *Slough system draining muskegs, forest ponds, forest floor run-off
Thistle	Glacial-drainage river
Barco	Lacogene river Blackwater pond and run-off drainage
Goose	Intermittent stream draining shallow tundra ponds

Saltwater features	Saltwater temperature, ice content
Two bays open to ocean swell Gradual, sloping sandy bottoms	10^{o} - 12^{o} C Warmed by Japanese current No icebergs
*Silty cove, 8.8 m deep, depauperate mud bottom, sheltered by sand bar from open swell Fjord harbour exposed to wind and swell	10^{o} - 12^{o} C Warmed by Japanese current No icebergs
*Lagoon 8 m deep Coves, channels *Tidal flux 4 km up "rivercourse"	7^{o} - 8^{o} C Iceberg injection infrequent Single-berg injection
*Small circular cove 8.6 m deep, channel between cove and open inlet	5^{o} - 6^{o} C. Iceberg injection daily Multiple-berg injection

(Continued

TABLE 2. (Continued)

Pod name	Vegetational/successional
Boussole	1400-year-old sp-he-mt forest, trees to 750 yr age, 26 m ht. Alder and Elymus zone fringes forest at beaches, but not along watercourse
Thistle	Sp-he-mt forest similar to above, trees 20 m ht, not so old. New cottonwood growth >60 yr old, on flood-scoured river. Alder and Elymus zone fringe all beaches and watercourses; willows on river flats
Barco	180-yr sp-he forest, trees to 20 m ht Alder and Elymus zones fringe all beaches, watercourses
Goose	50-yr successional stand, red alder thicket to 3.5 m, willows

Biogeographic status	Catastrophic features
Biogeographic island, isolated by icecap, tidewater glaciers, and sea. Access only from other parts of "island"	Violent sea storms (∿1/2 yr) sweep beach, deposit benthic organisms from 100 m below water level to 800 m inland from water line, eliminate small mammals resident in beach grass Seismic shocks regular (∿1-2/1 mo)
Same as above	Jötulhlaupir (∿2/century) Seismic shocks regular (∿1-2/1 mo) Freezing of freshwater lens in Thistle Cove (∿1/2 yr)
Access to continental mainland. Forest and mammal populations continuous with mainland	Pan ice freezing (does not block cove) Seismic shocks frequent (∿1/2-3 mo)
75% surrounded by flowing glaciers impeding most mammal movement. Indirect access to *mainland*	Iceberg accumulation blocks cove (incidental) Seismic shocks infrequent (∿1/3 *mos*)

(Continued

TABLE 2. (Continued)

Pod name	Human history and impact		Otter feeding sites	Otter retreats
Boussole	No known historic or present occupancy		Random river and forest floor sites No middens, no altars	2 dens within forest cover Ponds in sloughs
Thistle	Tlinkit residence and subsistence	? - 1892	Two altars	2 dens within forest cover
	Fish barge and trapping	∿1940 - 1960	Random sites on talus and gravel beach	1 den on top of cliff
	Fishing activity, spring/summer	1940 - pres		
Barco	Tlinkit residence	? - 1650	Man-made dock in lagoon	2 dens within forest cover
		∿1830 - 1899		
	Euramerican settlement	1882 - 1899	Random sites, gravel beach No altars	
	(15 km away)	1916 - pres		
	(on site)	1952 - pres		
	Tourism (increasing intensity)	1882 - 1899		
		1965 - pres		
Goose	Tlinkit hunting	∿1936 -∿1974	Ledge on rock face	No dens (summer)
	NPS ranger station	1965 - pres	One "shetiyyah" (III.3)	Retreat ledge on cliff face
	Tourism (increasing intensity)	1970 - pres	Random sites on beach gravel	

Key to symbols:

*	Focal water	Sp-he	Spruce-hemlock forest
+	Greatest amount of use by otters, relative to other types listed	Sp-he-mt	Spruce-hemlock-mountain hemlock forest

(Duggins and Quinn 1975). An example of this was furnished in the summer of 1978 by the sudden, widespread appearance of huge numbers of Salpa fusiformis at the Pacific entry of Icy Strait. The only previous record of such a massive florescence of salps, twelve years before, involved much smaller numbers (Bruce Wing, National Marine Fisheries Service, Juneau, Ak., pers. comm.).

The commonest benthic and pelagic crustaceans in the Pacific waters are pandalid shrimp, isopods, and gammarid and caprellid amphipods. Decapods and other orders are less numerous. Holothurians, echinoids, echiuroids, sponges, anthozoans, and limpets are abundant on rocky bottoms and cliffs. The silty bottoms of most of the inlets are depauperate in all species.

Mussels, barnacles, and colonial hydrozoans encrust the rocks of the intertidal and subtidal zones. Jellyfish (Aurelia and other genera) are commonly seen throughout summer and autumn, often in large shoals. Similarly large masses wash up on the beaches in October and November.

Although the sandy bottoms of Boussole Bay and Astrolabe Bay do not support a sessile fauna, violent storms precipitate a number of deepwater forms onto these beaches at wide intervals (1 in 2 yr observed). Serpulid and sabellid worms, tunicates, sponges, Nereocystis, and others, may be deposited above high tide line when a wrack of shallower-water algae is driven as much as 800 m inland from this line.

Such animals are apparently confined to bottoms beyond the outer limit of silt deposition in Boussole Bay, 100 m from shore. In Dixon Harbour, which, unlike Boussole Bay, is continually filling with silt, no such wash-ups after storms occur. In the autumn, as the result of seasonal die-off, all the beaches collect large numbers of crabs, coelenterates, and other organisms.

The Dungeness crabs, Cancer magister, are accounted "not particularly common" (Duggins and Quinn 1975), but they are taken daily and in some numbers by mink, otters, and sea birds throughout the year. Blennies, gunnels, and sculpins are found among the rocks and on bottom sands. Larger osteichthyan fish are not often found near shore, except when salmon run up the rivers. There are some flatfish (e.g. Platichthys stellatus) and sticklebacks (Gasterosteus aculeatus), which move between fresh and salt water, but they occur at low frequency (Murrell 1975).

The productivity of the Pacific shore is directly related to the shore's function as a repository for detritus brought in by the Japanese current, or dislodged from greater depths during storms. Along the sandy beaches, such detritus composes a major proportion of the biomass, and is critical for the survival of beach-scavenging mammals, including otters. In protected waters such as Thistle Cove, loons, ducks, mink, and otters forage daily, in large numbers.

As I noted in an earlier study, during the winter

when small mammal populations reached the lowest point of their decline along this coast,

> . . .as mink thinned out in inland ranges, their incidence on the beaches remained constant, while other inland predators, such as marten and weasels, dwindled or disappeared altogether. Predators having no capacity to utilise the marine food base available as detritus suffered in consequence. Those which were principally beach scavengers (otters, mink, wolves) or facultatively so (wolverine) managed to survive with no loss of numbers (Home 1977).

The populations of species which are preyed upon by marine mammals foraging entirely underwater must also undergo fluctuations, but the causative factors remain unknown. Harbour seals (Phoca vitulina) were observed almost daily in Thistle Cove during the winter 1973-74, and almost never in the winter 1974-75. Occasional sea lions (Eumetopias jubatus) swim ashore (or wash in dead) along the Boussole and Astrolabe beaches in the winter, after the majority of these animals have left the area.

On rare winter occasions, humpback whales (Megaptera novaeangliae) feed in these bays, in the same areas in which otters have been active. Whales are seen only much farther from shore in summer (Patten 1975). Killer whales (Orcinus orca), harbour porpoises (Phocoena phocoena), and other odontocetes are seen chiefly in summer, and rarely in winter. Grey whales (Eschrichtius robustus) pass close by this coast in the spring migrations (between 19 March and 9 May), and in fall (no data on the specifics of their appearance), and are very rarely sighted in mid-summer. Other species (right

whales, Baird's beaked whale, etc.) have been seen once in ten or twenty years (Home 1973).

The diversity of the terrestrial fauna on the Pacific coast here is low. Three species of shrews, Sorex cinereus, S. palustris, and S. obscurus, and three of small rodents, Microtus oeconomus, M. longicaudus, and Clethrionomys rutilus, and the red squirrel, Tamasciurus hudsonicus, occur. Otter, mink, marten, and weasels (Mustela erminea and M. frenata) are common animals when populations of these small rodents are at a cyclic high. The wolverine is represented by a single individual which crosses these two valleys each week, exploiting a total range almost seven times the diameter of those valleys. The wolf population consists of four. Foxes are rare (Home 1973, 1977).

Those mammal species which do breed in the area appear to have low rates of reproduction. The wolves copulate every March, but no cubs are seen for years at a time (Home 1977). The low number of summer sightings of mink and marten litters indicates low reproductive rates (Streveler 1975, 1977).

The coastal rain forest, which, as a biome, I have designated asgutu (Tlinkit, "forest") (Home 1977), is considered a low-energy ecosystem largely because of the slow rates of nutrient turnover (Waring and Franklin 1979). This term may apply not only to the silvic system, but to all ecological components in this ocean-coastal system. I have discussed many of these factors

elsewhere, and will quote only one summary statement here which is applicable to mammals:

> Predation is relatively strong, and populations may be affected adversely to relatively small degrees by other environmental factors, and then rendered disproportionately subject to predatory reductions much more quickly than in zones where such difficult periods as the persistent rains or vegetal freezing are less significant. It seems probable that the food base is generally limited, and that numbers of animals either never become very great, proportional to the territory involved, or that the food share per animal is reduced (in view especially of the very scanty crop of winter scats); the slopes of the food pyramids in the area may be much more extreme and eccentric than are expected in many inland populations. Many individuals of these species have body sizes somewhat under those observed in other parts of Glacier Bay; but some predators are found in numbers higher than in control sectors of the preserve (Home 1977).

These latter sectors are much modified by human activity.

But human activity has been modifying all of the study areas of the Pacific coast and within Glacier Bay for a longer time than many extant mammalian species have been present there. Human occupation of the Glacier Bay area dates back 10,000 years in Groundhog Bay, east of Point Gustavus (R. Ackermann, pers. comm.). The Tlinkits have lived in this area since 1400 A.D., and probably longer, since conquering their predecessors, the Eyaks, the duration of which in this area is unknown (De Laguna 1972). The Tlinkits were settled in villages and utilised subsistence camps, along the entire length of the Pacific coast until the late nineteenth century, when smallpox epidemics decimated their settlements (De Laguna 1972). Colonisation of various parts of the Glacier Bay reserve by small

numbers of Euramericans have been sparse and discontinuous since 1882, but today there are resident populations in Gustavus and Bartlett Cove, and sporadically continuous sites along the Pacific coast, particularly Lituya Bay, for mining purposes.

C. Biochronological Zones

On the basis of the historic succession of the forests since deglaciation, the Glacier Bay reserve contains six discrete "biochronological zones." All these zones contain resident otters, but the detailed studies reported here have sampled only three of the six.

These zones are: (1) the oldest, unglaciated for at least 11,000 years, represented by Dundas Bay (Streveler and Paige 1971); (2) the second zone, represented by the Pacific coast (below), has been unglaciated for 1,440 years; (3) the depositional plain extending from Gustavus to Excursion Ridge, not glaciated during the Little Ice Age; (4) the lower shores of Glacier Bay, unglaciated since 1800 A.D., represented by Bartlett Cove (below); (5) the shores of Muir Inlet to the still-glaciated areas (none of the bare rock has been ice-free longer than 90 years; and (6) the still-glaciated and most recently deglaciated areas, covered by no more than Dryas in its early stages - but predominantly vegetation-free.

The Dundas Bay zone exhibits a spruce-hemlock forest containing yellow cedar, unique to this zone. The diversity of herbs

and forbs here is greater than that found in any other forest zone.

The second zone is that of Boussole Bay and Dixon Harbour.

The third zone, the Gustavus foreplain, was probably not forested during the Little Ice Age (Streveler and Paige 1971). The existing forest, probably dating only since 1800 A.D., has few spruce and is dominated by lodgepole pine (Pinus contorta), not seen elsewhere in the reserve. Individual trees are smaller, and the forest sparser and more open, than the forests elsewhere in the reserve. The soil seems to have been impoverished by glacial leaching.

The Gustavus plain is covered by watercourses which provide habitat for aquatic mammals, including beavers, water shrews, mink, and otters. The otters in the Salmon River have never been seen in the sea south of Gustavus, or along the shore. The shore, principally mud and sand, is the type least often used by otters (Tables 2 and 3). Tidewater invades the Salmon River to 3 km north of shore line, and the otters are active in the lower river at those times.

The Gustavus forest is continuous with the spruce-hemlock forests to the west shore of Lynn Canal. The composition of mammal species in the area differs from year to year in numbers and incidence of species, for reasons not adequately understood. All species ranges are changing rapidly at present because of the increase of human settlement in Gustavus.

TABLE 3. ENVIRONMENTS OF OTTER PODS NOT STUDIED IN DETAIL (Key to symbols on page 116)

Pod	Coastal type	Beach type	Freshwater feature	Vegetation
Palma Bay	Open Pacific, tidal *slough system	Gravel, rock face with talus	*Glacial river	Beach grass Sp-he forest
Torch Bay	*Sheltered Pacific bay	Rock face, talus, gravel beach	Small run-off streams from slope	Sp-he forest Grass fringe
Lituya Bay	*Sheltered fjord	Rock face, talus, gravel beach	Ponds on island	Sp-he forest (often removed)
Dundas Bay (east)	Sheltered shallow bay	Gravel and mud beaches, grassy flats	*Lacogene river	Grass flats Mature 11,000 yr forest
Gustavus	No use made	Mud, sand (not used)	*Lacogene river	Pine forest
Geikie Inlet	Open Glacier Bay coast	Rocks, gravel beach, boulders	*Lacogene river	Sp-he forest
Sebree Cove	Sheltered Glacier Bay coast	Rock face, talus, gravel beaches	No freshwater	Sp-he forest maturing
Adams Inlet	*Sheltered Glacier Bay coast	Gravel beaches, boulders	Glacial river	Alder-willow Sp forest developing
Rowlee Point	*Open glacial fjord coast	Rock face, boulders, gravel beach	No freshwater	Alder, grass
Tidal Inlet	Sheltered glacial fjord	Rock face, boulders, gravel beach	Glacial melt	Willow-alder

(Continued

TABLE 3. (Continued)

Pod	Coastal type	Beach type	Freshwater feature	Vegetation
Anita Bay	Sheltered archipelagic bay	Rock face, boulders, gravel beach, mud	*Lacogene river	Sp-he forest Grass flats
Brownson Island	*Inland salt chuck	Rock face	Small streams, pond drainage	Sp-he forest mature and varied

Location

Page 115, all sites are located within Glacier Bay National Monument

Page 116, Anita Bay is on the north coast of Etolin Island; Brownson Island is east of Etolin Island.

Symbols

*	Focal water for pod (not identified in every case)
Sp	Spruce forest
Sp-he	Spruce-hemlock forest
Lacogene	Freshwater drainage originating in lakes, ponds, or other non-glacial features, not carrying glacial silt

Bartlett Cove represents the fourth biochronological zone, covered with ice during the Little Ice Age and deglaciated now for 180 years. This is the habitat of the only kushta pod I have studied which has no rock cliffs, domes, or talus in its range.

The most nearly periglacial of all otter habitats is the fifth zone (the sixth is invaded only occasionally). I include in this zone all the area north of Muir Point in Muir Inlet, and all of the area of Tarr Inlet, north of the mouth of Tidal Inlet. None of these sites have been ice-free for more than 90 years. Goose Cove, deglaciated for 53 years, is the sample study site.

In upper Tarr Inlet, otter sign has been found in Reid Inlet, as little as 200 m from the face of tidewater Reid Glacier (Home 1973). This is not the sign of a resident pod. Three otters were seen on a rock within 1 km of the faces of Grand Pacific and Margerie Glaciers, at the northern terminus of Tarr Inlet in mid-July, 1978. The waters here have a mean summer temperature of 3^{o} C, and are filled with icebergs.

In Muir Inlet, the Goose Cove and Rowlee Point pods are the most nearly periglacial of any resident otters presently known. The two pods occupy the east and west inlet shores directly opposite each other, separated by 4 km of water. A distinct pod inhabited Nunatak Cove, north of Goose Cove, from 1967 to 1969. The face of Muir Glacier was then 16.3 km north of Nunatak Cove. In 1978, when the face of Muir Glacier was 34.3 km north of Goose

Cove, there were no otters in Nunatak Cove.

NPS rangers Cornelius' and Wik's logs indicate that the range and activities of the Goose Cove and Rowlee Point pods were about the same in 1968, 1969, and 1971, as they are today. Given the observed conservatism of range in these and other pods studied, and that of other kushta pods, it is possible that the Rowlee pod has been active in Wachusett Inlet as far north during previous years as I observed it to be in 1978. I saw the male 11.3 km north of the mouth of the inlet. In 1968, an otter at a similar position would have been swimming in water 4 km from the face of Plateau Glacier. This dead glacier has since then collapsed and melted rapidly. Today, the face of its remnant is 9 km from the point of sighting.

The degree of glacial retreat, and consequent warming and iceberg-depletion of inlet waters, seems not to be a decisive factor in otter settlement or exploitation.

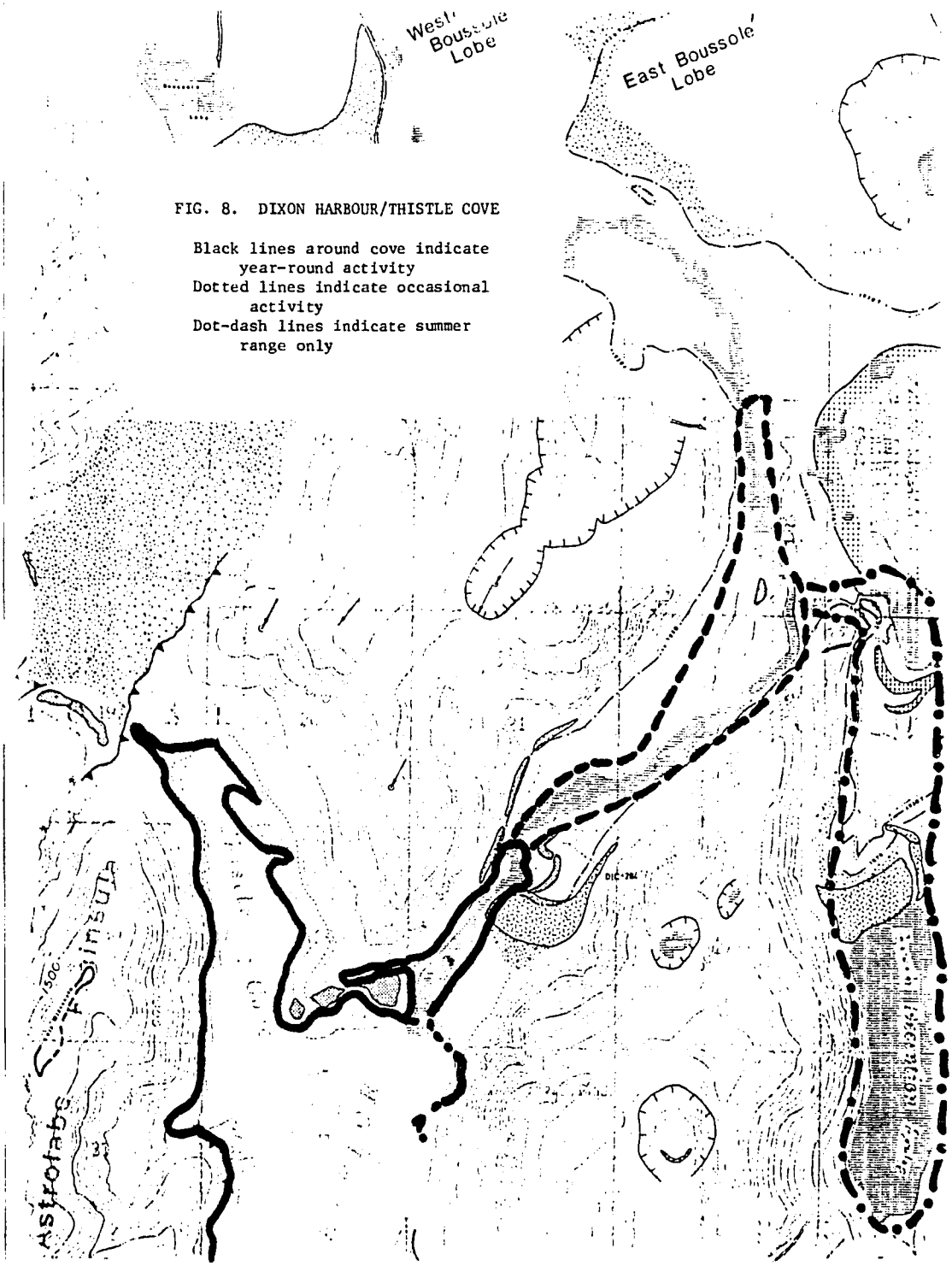


FIG. 8. DIXON HARBOUR/THISTLE COVE

Black lines around cove indicate year-round activity
Dotted lines indicate occasional activity
Dot-dash lines indicate summer range only

II.2. THE CHARACTER OF INDIVIDUAL POD RANGES

A. The Question of Territoriality

Solf (1972) believed that Alaskan otters had no exclusive territories, and that fighting among pods, for territorial or other reasons, was rare.

In 1969, NPS ranger Cornelius's log recorded a pod (two adults, two kits) in Goose Cove at the same time as the resident pod (two adults, one kit), with easy interassociation. The visiting pod may have come from Nunatak Cove, or from Rowlee Point. It is the only record of such a visit anywhere in Glacier Bay.

Inland otters, of both European and American species, seem to be alike in that the territory of males, on the one hand, and of females and kits, on the other, are separate, although there is considerable overlap between the two. The dens of each sex may be close together (Liers 1951, Erlinge 1967). Reports to this effect do not indicate whether the female/kit territory is entirely subsumed into that of the male, as it is in Alaska. Grinnell (et al. 1937) believed that the male of California maritime pods was always with, or near, the rest of the family, and that this was the rule, not the exception. Novikov (1956) acknowledged that an undisclosed proportion of inland Eurasian otter pods remained in interassociation most of the time, and that the male participated in training the kits.

The two statements preceding describe the situation I have observed in all kushta pods for which I have data. Consistency of pod association, which occurs facultatively among inland populations, is selected for positively in maritime habitats (IV.2, below). Although there is a difference in the total area of the range exploited by the female and kits, relative to the male, the female/kit range is entirely included within the male's territory.

Erlinge (1967, 1968) discovered that females and kits of inland Swedish otters occupied different territories from that of the male during the summer. In summer, all territories were at their smallest, in terms of weekly activities. The male had a much greater range both in diurnal and nocturnal activity. The range of the female/kit group became extended in the course of the year.

Swedish female otters with kits travelled 3 to 4 km per night in winter, and more in spring. Males sometimes moved 10 km per night. Erlinge acknowledged that this disparate territoriality was not characteristic of British or American otters.

Stephens (1957) found sexual segregation between the dens of some British otters. Liers (1951) acknowledged a similar arrangement in the dens of wild L. canadensis, but felt that the differences between the extent of territory, and the nightly movements, of the two sexes, was less distinct in a pair of American otters compared to European otters.

Erlinge considered the use of scats to mark territorial boundaries to be habitual. Such a habit was not found among Scottish maritime otters (Elmhirst 1938) nor with Alaskan kushta otters. Scat markers do have territorial implications for kushta otters (III.3, below). Scat deposits on habitual feeding sites and other features in the focal water have a territorial connotation. Streveler (1977) believed the Thistle pod sometimes left scats at mink dens in summer. I did not observe this in winter.

In other areas, where otter populations are dense and all pods' territories abut others, scat markers may be deposited along boundaries. On the Alaskan coast, there is often no geographical feature distinguishing the interface between pod activities; indeed, pod ranges often do not contact others at all. No need for territorial markers on range frontiers exists. The negative response shown by the pods I have studied to the action of removing or interfering with their scats at sites around their focal water is probably a vestige of the old (or facultative) association between scats and territorial claims developed among inland populations.

Erlinge found the range of some male otters to be as wide as 15 km, depending upon topography and the frequency of other males in the area. In Sweden, the centres of home ranges averaged 6 to 8 km apart. When a lake was included in the range of one male, that male might cover a linear distance up to 7 km in one day's journey. If the range contained only streams, the daily linear distance reached an average of 11 km.

In Britain, Stephens (1957) found that the home ranges of females with kits, or of whole pods, averaged 8 km in diameter. She considered streamside pods only.

In optimal Swedish habitats, Erlinge (1968) found otters concentrated in the proportion of 1 otter/2-3 km lakeshore, or 1 otter/5 km of stream. He believed that males (and complete pods) covered from 1/3 to 1/4 of their territory every 24 hr period. Three or four nights were required to cover the entire range. Ranges were smallest in winter and summer, when activities were restricted to favourite spots. In spring and autumn, the animals were much more mobile. Families sometimes disbanded in spring and summer.

At any time of year, Erlinge found the incidence of activity unequal throughout pod ranges. Most otters spent most of their time in the water body which is the centre of their range. This site of concentrated pod activity, whether a stream, pond, lake, or marine bay, is what I term the "focal water" (=ottery of other authors).

Erlinge (1967, 1968) and Stephens (1957) found that all otters moved night after night, and, except when the female was still nursing kits, rarely denned twice in the same place. This is not true of kushta otters.

To summarise, territoriality is a very active factor in the behaviour of inland otters, but has only a vestigial function, not likely to stimulate defensiveness, among the pods here studied, and probably generally among those of coastal regions.

B. Dixon Harbour/Thistle Cove, and the Thistle Pod

Details of the significant environmental parameters of the four major study sites are tabulated in Table 2. Only those variables not apparent from the table will be detailed below.

Dixon Harbour, 3.6 km in length, is the longest fjord on the southern Pacific coastline of Glacier Bay reserve. Its total water area of 7.9 km^2 is exposed to the prevailing southeast winds and swells of the Pacific.

In 1973-75, the water area of Thistle Cove at mean tide level was 3.8 km^2. Thistle Cove (Fig. 8) has no freshwater influx except for small muskeg-draining streams, and rain run-off. Clay and sand bars close this cove from Dixon Harbour, and the swells of the harbour do not extend into the cove. The cove receives a continuous back-eddy of silt from the discharge of the Dixon River, and the cove's depth decreases annually, as the bars at its mouth grow larger at the same rate.

Once in two winters the freshwater lens over the surface of Thistle Cove froze completely, without patches, and remained frozen across the entire cove for ten days. During the solstitial tides, the cove is nearly emptied of water, and the bottom can be examined on foot. During the rest of the year, the water at lower low tide level is 8.8 m at the deepest point.

Most of the freshwater lens on the surface of the cove probably originates from the Dixon River. This river drains

the ice-dammed Dixon Lake on the fringe of Brady Icecap, the glacially-fed North Deception, and the clearwater South Deception Lakes. The Dixon ice dam broke just before 1894, and again around 1920. The resulting jötulhlaupir swept the lower Dixon Valley clear of vegetation each time (Derksen 1975). At river level today, cottonwoods and alders are younger and more numerous than elsewhere on the coast. Above the level of the jötulhlaup floodwaters, the vegetation is similar to that of adjacent areas.

Thistle Cove was probably not affected by these floods, except for a backwash of tree trunks and debris. The periglacial lakes around the Dixon drainage also rise and fall from year to year, and season to season, providing some modest overflow flooding (Derksen 1975).

The Dixon River is much braided, especially through the centre of the valley covered by gravel flats which bear alder thickets and willows. This valley averages 1.66 km in width. Spruce forest encloses the lower course of the river and, along the periphery of the gravel flats, extends 11.5 km inland from the sea. From that point to the flanks of Brady Icecap the gravels are bare.

At low tide the river averages 4 to 5 km in width in its lower course. Steady winds blow across the valley from the Brady Icecap in winter, and freeze the central third of the flats solid. The lower 0.7 km course of the river remains ice-free, as it is tidally infused. The breakout of the water from beneath the ice

is the usual limit of otter activity along the course of this river in winter, but the otters on occasion penetrate farther.

Some side channels and pools of the Dixon are clear, and suitable fish habitat. There are small clear tributaries to the river.

Segments of the river in the upper third of the valley remain ice-free during most of the winter. Snow banks rise sheer as much as 2 m above its banks.

Even the turbid sections of the Dixon are inhabited by several species of fish. Runs of eulachon (Thaleichthys pacificus) are documented in March. There may also be a steelhead (Salmo gairdnerii) run at the same time. Other salmon species move through the river to the Deception Lakes in September. Coho (Oncorhynchus kisutch) have been taken from the river (Murrell 1975).

Salmonid skulls and bones, sometimes unidentifiable as to species, and cottid bones in smaller numbers, are found at otter feeding sites and in scat. Cod (Gadus macrocephalus) is sometimes present in large numbers in the harbour. I observed mink fishing both capelins (Mallotus villosus) and herring (Clupea harengus) during winter.

Dungeness crabs (Cancer magister) are not as numerous as in Glacier Bay itself, but there are enough in Thistle Cove to provide daily fare for five otters, three mink, and hundreds of loons and goldeneyes. Otherwise, the invertebrate fauna of the cove is depauperate (Mueller et al. 1977).

Because the cove is sheltered, it is utilised more heavily in winters by feeding sea birds than is any other bay along the coast. Over two winters, species incidence and frequency of use in Boussole Bay and Astrolabe Bay taken together constituted only 0.2% of the activity in Thistle Cove (Home 1977).

Arctic and common loons, horned grebes, pelagic cormorants, Barrow's goldeneyes, buffleheads, surf scoters, common scoters, red-breasted mergansers, glaucous-winged gulls, mew gulls, common murres, are seen in numbers ranging from one to three hundred almost every day in winter. Many other species are observed less frequently. Only the ten days' formation of pan ice in the winter 1973-74 forced all species of birds and mammals usually found inside the cove out into the waters of the open harbour, when temperatures were lowest, and winds fiercest, of the two winters.

Evidence for the activity of mink, otter, and small mammals is much greater on the western side of Thistle Cove - a rock face with gravel beach - than on the eastern side, which is an expanse of mud and sand flats.

Wolves move along the eastern shore in winter, but hunt both shores in summer. The wolverine circles the cove completely around the year. Bald eagles are always present perched on trees near shore, but are in low density until the fish runs of March. There are no other large avian predators.

Human activity has a discontinuous history here (Table 2). Fishermen utilise the cove today from late March to September of each year. In the 1970's, fishermen coming into the cove were prone to shoot bald eagles and sea lions, and probably anything else that moves. The otters evidently withstand these depredations.

Thistle Cove was the focal water of this pod, and the otters were active in it daily, except for absences of two or three weeks at a time in April, 1975. Only when the cove was covered by pan ice, or emptied by solstitial tides, or when there were harbour seals in the cove, were the otters absent from it at other times.

The female and kits were active on the water and along the shore. The male frequently tracked into the forest in the winter 1973-74, when small mammals were numerous, but rarely did so in 1974-75, when small mammals were scarce. The female and kits never tracked more than 30 m from the waterline, and that rarely. The male moved as much as 120 m from waterline, tracking up and down steep slopes without reference to watercourses. He often moved parallel to the waterline of the cove along the slopes.

On occasion, one otter (the male) moved to the top of the saddle between Thistle Cove and Astrolabe Bay. He never went as far as the edge of the escarpment, and so did not encounter the Boussole male, which climbed the cliff (C, below). The Thistle male, mounting a gentle slope to an altitude of 95 m, made only two or three ascents each winter. Neither the female nor the kits

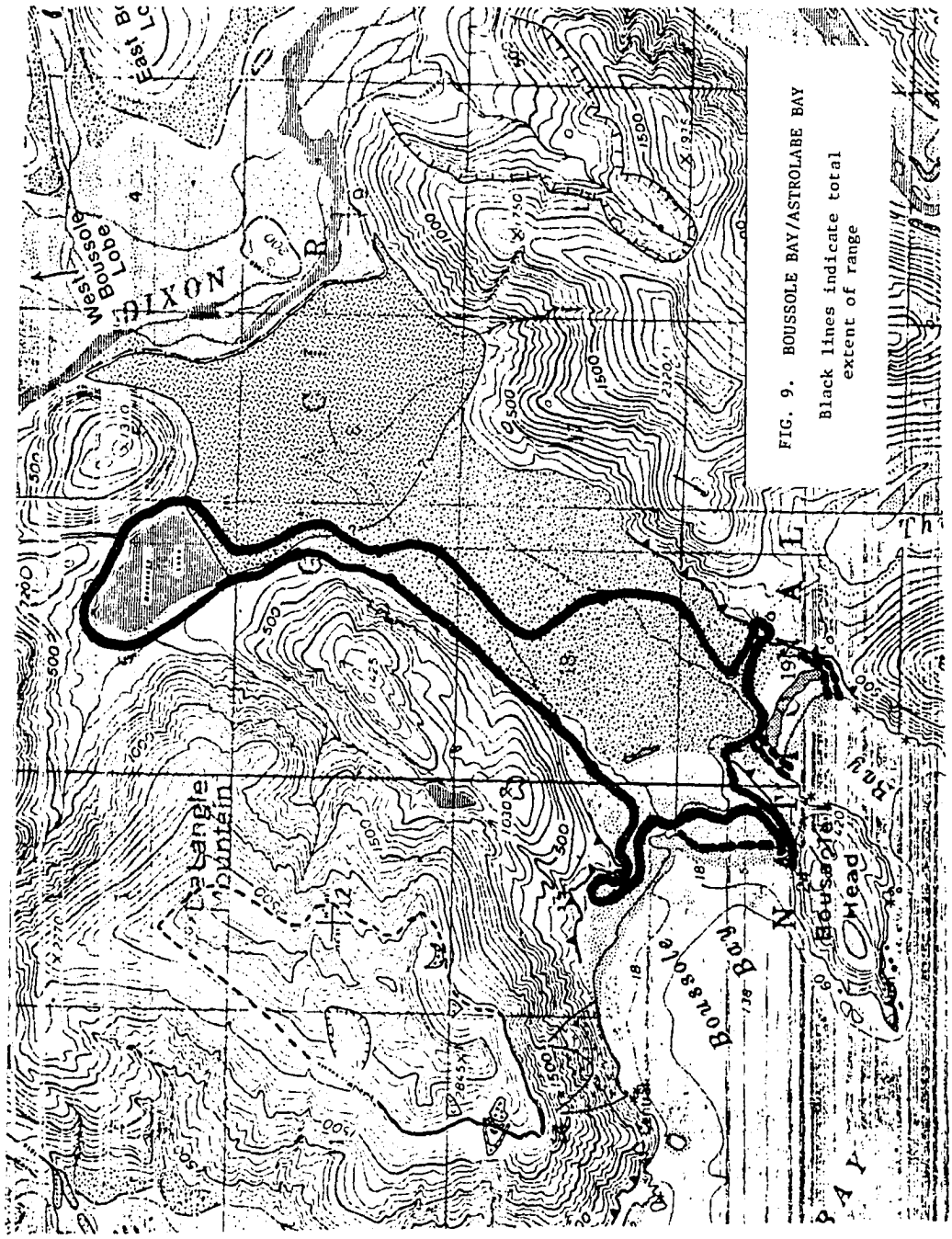


FIG. 9. BOUSSOLE BAY/ASTROLABE BAY

Black lines indicate total extent of range

ever made shore forays as much as 12 m in elevation.

The entire pod sometimes crossed the sandy, detritus-littered Dixon Beach, 0.5 km wide, zigzagging from sea edge as far as 200 m from the water. The otters hunted ponds and streams behind the dunes, and within the forest, but reached these from channels draining into the Dixon River, and not from the beach.

The pod was active an average of once every three days along the lower course of the Dixon River as far as the ice breakout. A freshwater stream enters the Dixon at this point, and the pod moved 30 to 40 m up the course of this stream.

A single otter (the male) went as far as 6.5 km up river from the mouth of the Dixon at a frequency of about once weekly in winter. This otter crossed the ice bridges of the river's frozen segments, sometimes falling through the ice in the process, and swimming under the ice to the next clear sector. At times, this otter moved to the ice-free sections through the alder thickets by way of the freshwater tributary mentioned.

Once or twice each winter this otter travelled as far as 12.4 km upstream from the mouth of the Dixon. About half of this distance was covered entirely in the water.

There was a den on top of a sheer sea cliff 3.7 km south of the mouth of Thistle Cove. The 25 m cliff was often covered with frozen spray. On two occasions each winter, birds were eaten at the mouth of this den, and otter tracks were in evidence.

The climb had evidently been made straight up the cliff. There was no evidence for more than one otter.

Probably only a single otter also climbed cliffs around frozen waterfalls on the east side of Dixon Harbour, to heights of 15 and 18 m. There was evidence on some occasions for several climbs, but all were probably the trace of one animal. Above these cliffs were forests hunted by other mustelids, which must have been populous with small mammals, but the otter did not hunt through it at any time I observed the climbing traces.

No otter went into the frozen Deception Lakes in winter, or moved along the drainages between these lakes and the Dixon River. In summer, otters and otter sign were found all along these drainages and around North and South Deception Lakes. Dens were found around the shore of South Deception Lake (Streveler 1977).

Two altars (III.3.C, below) existed in Thistle Cove. One was a high sarsen at the north end of the cove, still dry on its northern side at all but the highest tides. The other was a rock promontory at mid-point on the west side of the cove. The otters used these altars very little during the two winters, and never left scats there. In summer, when human observers were less frequently in the area, the otters made more use of the altars (Streveler 1975, 1977).

Random feeding remains were commonly left around the shores of Thistle Cove. Random sign was rarely found elsewhere.

In the summer, random sign was less frequent and more remains were found on the altars (Streveler 1977).

I located two dens, neither of which were used during the winter, although the otters sometimes moved to, but then past, one. Both were located inside the forest line and were in the roots of spruce. One, near the promontory altar, was 8 m within the forest line. The other, already described, was at the top of a cliff, and near the edge (the tree stood at the edge). The otters occupied a third den somewhere in the boulder-tumbled sheer cliff on the southwest side of Thistle Cove which I could not approach from water level or from the summit.

Documentation of the range for the female and kits indicates that these otters spent almost all of their time in Thistle Cove, at the lower Dixon, and along the beach and harbour waters between. In summer, the otters extended their range considerably by entering the Deception Lakes and exhibiting activity around all of the shores.

The male's range was very much greater, extending 3.7 km south of the mouth of Thistle Cove along sea cliffs, and 12.4 km upstream of the Dixon River from sea line. I do not know whether the male also went southward on the east side of the harbour.

It is unlikely that any of the otters swam out into the open waters of the harbour far from the cliffs, as I have not observed otters to swim away from shore except on rare occasions (young individuals sometimes do so).

The total area of salt water used by all otters, particularly the male, in both Dixon Harbour and Thistle Cove, I estimate at 9.3 km^2. The land and river area of Dixon beach, Dixon River, and the valley flats is 11.7 km^2. For summer only, the Deception Lakes and their drainages within the ambit of otter activity cover 10 km^2.

In summer only, 9.3 km^2 of saltwater and 21.7 km^2 of river/overland was covered by the male. In winter, the saltwater area remains the same, and the river/inland area is reduced to 11.7 km^2.

Concentrated activity for the male is coincident with the same area used by the female and kits. In winter this was 4.4 km^2 of salt water, and 3.0 km^2 of river/inland range. In summer, the female and kits expand their range into the Deception Lakes, and thus range over 13 km^2 river/inland.

The area of Thistle Cove comprises only 11.8% of the male's total winter range, but is the site of about 60% of the pod's activity during sample weeks in winter, and perhaps more. (The pod was often active in the water without leaving any sign on shore.)

The female and kits were active in a range of about 35.6% that of the male's winter range. Parameters of the summer can not be determined, but single otters (probably the male wandering alone at all times, but perhaps not - see below) were sighted in remote parts of the valley.

The total linear coastline exploited by this pod was thus 6.8 km, but only 3.4 km was the scene of regular activity.

C. Boussole Bay/Astrolabe Bay and the Boussole Pod

These two bays (Fig. 9) are part of a single geographic formation, the beach of the Boussole Valley. Boussole Head, a gabbro-diorite dome 120 m in elevation, separates this otherwise continuous beach into two bays. The Head does not extend into the valley, which has a flat, poorly drained floor.

The beaches are sandy. Boussole beach is 1.5 km long, and 800 m wide from water line (at mean tide) to the alder zone. The beach is scoured by prevailing winds, and there are no permanent sand features. Astrolabe beach is protected by the forest from the icecap winds, and dunes have formed along its entire length.

There is no freshwater drainage into Astrolabe Bay, and the otters entered this beach only rarely. All of the valley's streams flow west into the Yay River, which discharges into Boussole Bay. Most of the valley floor drains into a slough system, the Kit Creek sloughs, which, along with the lower course of the Yay, is tidally infused. The Yay River is flooded to as much as 0.4 km inland at mean high tide, and 75% of the area of Boussole beach is covered by water, relative to lower low water line.

The valley is 2.5 km in mean width, and 9.4 km in length. On east and west the valley is hemmed by sheer cliffs, and on the

north is bounded by the Dixon River.

The minimum elevation of the eastern cliff is 90 m. This cliff, nearly sheer, is climbed by the otters to its summit. The western cliff is part of Delangle Mountain, with a minimum elevation of 400 m, and is not approached by the otters.

Boussole Head is covered by krummholz, chiefly mountain hemlock. Throughout the winter the summit is hunted by marten and mink. Otters never move over the summit. Its sheer rock walls, from 3 m to 10 m high, divide the beaches. Otters move to the sea from the slough system only along these rock walls, returning by the same route. At low tide, the cliffs at sea level are 12 m high, and the water along them 19 m deep, the deepest anywhere in the bay. This is the only part of the bay in which otters fish. The bottom away from the rock consists of continually resorted sand sloping gradually out to sea.

The absence of any other foraging animals in the open waters of this bay or of Astrolabe Bay, indicates an almost total absence of any prey populations away from the sides of the rock. Otters spend only 2 hr or less a day in the sea here, and probably do not forage anywhere except in the immediate vicinity of the rock.

Harbour seals are rarely seen in either bay. Sea lions appear occasionally, or wash in dead. I saw humpback whales feeding in Astrolabe Bay only once in two winters although the whales occur there fairly regularly in summer (Patten 1975).

Only individual sea birds are observed in the waters of either bay, and on rare occasions only. Compared to Thistle Cove, the nektic resources of these waters is poor. As a result, the otters make less use of the sea than does any other pod in my study.

The otters moved to the sea from the Kit Creek sloughs along a corridor 6 m wide, and 800 m long. On the few occasions when one or two otters moved into Astrolabe Bay, they did so along a similar corridor extending on the east side of Boussole Head from the sloughs to the beach, entered the water, and came ashore on the south side of the beach. The stimulus in this case was provided by the lure of a sea lion carcass which a bear had dragged behind the dunes on the south side of the beach. The otters (the two adults) moved straight to the carcass returned to the sea by the same route, swam north to the outward corridor and returned to the sloughs by the same route. There was no use of Astrolabe beach at any other time.

There is little gradient to the valley floor, and water flow is sluggish. The spruce-hemlock forest is broken by many muskegs, streams, and pools. Many of the streams are dry most of the winter. Others. although shallow, never freeze. The deepest sections of the Kit Creek freeze solidly. Only parts of the Yay River freeze in winter; there are always sections of ice-free water. The river's source, Lake Andromeda, is often frozen over.

Insect larvae (muscid, caddice-fly, etc.) are found in the river, and harvested through the winter by dippers. Dolly Varden (Salvelinus malma) and red, or sockeye, salmon (Oncorhynchus nerka) run the Yay River in September, and enter Lake Andromeda. In the river and more commonly, in the sloughs, are staghorn sculpin (Leptocottus armatus) and the starry flounder (Platichthys stellatus), both of which move in and out of fresh and salt water (Murrell 1975).

Water shrews occur in the river. When vole populations are high in numbers, mink, marten, and weasels are numerous and hunt the entire valley floor, as does one or more otters. Wolves and wolverine hunt the beaches and nearby forest zones, but rarely penetrate more than 0.5 km inland.

When vole populations decline, most of the inland valley becomes vacant of predators, except for the otters.

On the eastern valley wall is a talus slope of about 39^{o}, covered with devil's-club. This slope provides the only trail giving access to the summit of the escarpment, and it continues down to Thistle Cove. Wolves, wolverine, marten, mountain goats, and human observers must use this trail at all times of year, even though in late winter the ascent is covered by unbroken snow and is precipitous.

Forty meters north of this trail, a small pond drains over the escarpment lip down a sheer cliff into the valley. This cliff is often crusted with thin ice in winter, and the pond

itself is frozen continuously. One adult otter climbed the cliff around this drainage an average of once a month each winter. The otter's activity at the summit consisted entirely of standing on the pond ice a few meters from the edge of the cliff, and returning down the cliff. Of all other mammals, only the wolverine was able to duplicate this climb, and that only once. The otters were seen in the pond during the summer.

One otter climbed the other, main trail, only once, in April, 1975.

The trail proceeds northward to Palma Bay along the sea-front cliffs at the west end of Boussole Valley. The otter pod was only rarely active on the beach at this side of the valley, and never followed the trail. The otters were sometimes active in the alder zone and went into the small segments of the forest, to which the pond had access at high tide through river channels.

Daily activity of these otters, gauged by tracks on land, in snow, mud, or sand, was confined to the lower course of the Yay and to the Kit Creek sloughs in winter, with one avenue of approach to the sea. The river was traversed regularly to about 3.5 km from the beach line. About 4 to 5 linear km of the many sloughs were included in the focal water. The lower regions of these sloughs, which were infused with saltwater at each tide were the sites of the most concentrated activities.

Lake Andromeda, 7.8 km up river, was exploited only rarely in winter. The pod was not found to be active there for many

weeks at a time, although the otters moved up and down the river at least once a week, and sometimes more often. In September, during the red salmon run, the otters were active only in the rivers and around the lake, and fed only on salmon.

Not all of these otters went to the sea every day. Occasionally only one or two individuals went down the corridor. There was more evidence of separate activities on the part of the individuals in this pod - which in its range approximates more nearly that of an inland pod - than for any other coastal pod. The fact that the two adults deserted the kits to travel to Astrolabe Beach alone is unique (in this area); it may reflect a fear of predators around the carcass they sought.

The male hunted alone more frequently than did any other male, and covered vast amounts of overland territory every day. During the first winter, when vole populations were high, this male showed every sign of hunting activity, systematically checking each qamaniq. But his activity pattern remained the same the second winter, when vole populations dropped to near vanishing. In one 24 hr period I tracked him for 9.4 km linear distance, and he may have covered more distance within the watercourses.

Only once did the otters track across the sandy expanses of Boussole beach. On 11 November 1974, an exceptional storm deposited an enormous mass of wrack 800 m above low water line at the fringe of the alder zone. Five separate strand lines of benthic

and other marine organisms were spread across the surface of the beach. The wrack line, and most of the strand lines, averaged 1.3 km in length.

The pod moved together to inspect all the strand lines and other detritus on the beach. The otters scavenged most of the birds and some of the invertebrates (III.1, below). But the pod did not search the belt of wrack nearest the alder zone, since no otters ate the bird carcasses entangled there. Except when crossing the alder and grass zones on its way to the sea, this pod never entered those zones.

Although random feeding sites were observed both winter and summer, no middens, altars, or other regular feeding sites were observed. This is a feature in common with inland otters which also exploit marginal ranges (Field 1970). Two dens were found, one at the bend of the Yay River halfway to Lake Andromeda, and one on the north shore of Lake Andromeda, which was not used in winter. The den at the lake was in spruce roots within forest cover. The den on the river was in a sheer rock cliff. Regular shelter in the lower river, around the focal water, is not known.

These otters burrowed into the snowy banks along the sloughs to as much as 1.4 m during winter. These burrows were driven in against bank walls, and must have been for shelter.

I estimate maximum use of salt water around Boussole and Astrolabe beach at no more than 1.5 km^2, and probably much less. Daily use of Boussole Bay consisted of no more than 600 m^2 of water

and probably less. Total area of beach, river banks, and valley floor over which all otter tracks were observed was 22 km^2. Marginal territories (the escarpment pond, the area behind Astrolabe beach, and the once-only beach use) add only 3.4 km^2 to the above.

About 66% of the area of the entire valley floor was hunted through the winter. In any 24 hr period, less than 10% of the area showed evidence of activity, although the linear extent of such activity was often extensive.

This gives a total range for the male of 26.9 km^2.

The exact area exploited by the female and kits is more difficult to estimate, owing to the intricacy of the waterways and the absence of tracks along parts of the watercourses where the animals were active. John Rose and Ed Murrell (Wildlife and Fisheries Program, University of Alaska, pers. comm.) often observed the pod together in the summer (1974-1975) and saw the male come ashore on some occasions in which the female and kits remained in the water.

Adding all areas in which multiple tracks were observed, and the adjacent linear watercourses connecting them, I estimate a linear total of 4 km along the lower Yay, the Kit Creek sloughs, and the small area of Boussole beach as intensive use for the female and kits. In summer and September, Lake Andromeda is included. The total area of the river and sloughs then used is 10.5 km^2, or 39% of the male's range.

D. Bartlett Cove (Fig. 6) and the Barco Pod

Bartlett Cove is a younger environment than that of the Pacific coast, but because it is not isolated biogeographically from the Alaskan mainland, its fauna and flora are more diverse than are those of the Pacific fjord sites.

The Bartlett River flows from a forest lake through a broad, flat plain with little gradient, for 13 km from its ocean mouth. The river mouth is farther up the course of the river than appears from examination of the river's external features. Sea anemones, barnacles, and mussels live on rocks as far as 4 km from the apparent discharge of the river. Tidal infusion moves even farther upstream. and the hydrological limits of salt water along its course shift constantly.

The lagoon, which is the focal water of the Barco pod, is not part of the river system, but an inlet of the sea. Because of isostatic rebound, the lagoon is growing shallower annually. Unless there is a decrease in the present rate of rebound, this lagoon will cease to exist within thirty years of this writing (1981).

The river delta consists of a complex of islands, reefs, rocks, and shallows, with many narrow channels, and "secret coves" (confined by island masses and waters too shallow to be crossed by boats, over bottom too irregular or muddy to be walked). The total length of shoreline is enormous, and the total range of the pod is and will remain unknown. It is the segment of its range most regularly under human observation which is the zone of

concentrated activity for this pod.

The lagoon has a rich, well-studied fauna of echinoids, holothurians, anthozoans, mussels, crabs, other bivalves, several species of starfish, and swarms of small crustaceans. Species utilised for human food, such as Dungeness crabs and steamer clams, have been seriously depleted over the last decade by humans. Crabs are common in the Beardslee Islands and move from these islands into this lagoon at all times of the year. Dolly Varden, sticklebacks, and cottids are common in the lagoon. Because of the high incidence of human activity, sea birds make little use of the lagoon. Harbour seals enter it singly every other day or so.

Since human occupation of the Gustavus area began in 1916, brown bears have abandoned the Bartlett Cove-Gustavus region. Coyotes, first seen in 1919, have become numerous, while foxes have disappeared. Mink are no longer seen, but otters remain active in the lagoon daily (Home 1973).

When the first NPS cabin was constructed on the lagoon island in 1954, the Barco pod occupied a den in the forest on the east end of this island (the cabin was on the west end). Despite intensive construction of docks and buildings in 1958 and 1965, this pod did not abandon residence in this den until 1968 (Home 1973).

In summer, the pod's activities are modified by intense human competition, but the pod has never abandoned foraging in the lagoon for as much as three days in succession. In winter, the pod is observed in the lagoon almost daily.

From 1965 to 1977, the otters regularly carried their daily food catches from the lagoon to the floating boat dock to eat. They left large amounts of scat on one end of this dock. In 1977, the section covered with otter scat was removed. The otters ceased to defecate on the dock, but continued eating on it. However, they ate there less frequently. There was no change in the amount of their daily foraging otherwise.

In winter, pan ice sometimes forms on the north side of the lagoon. The otters often cross this ice single file, or attempt to climb up on it even as it breaks away beneath them. It is always possible for the otters to reach the shore without crossing the ice, but is evidently less fun for them elsewhere.

I have made many boating trips up this river and through its channels, and many hikes along its shores, from 1970 to 1978. I have never encountered this pod outside the lagoon area, nor has anyone else.

E. Goose Cove (Fig. 7) and the Goose Pod

The retreat of Muir Glacier was accelerated by the 1899 earthquake. In that year, Goose Cove was covered by 365 m of glacial ice. By 1925, the face of the glacier had begun to retract from the shallow bowl of gravel now known as Goose Cove; within two years, this cove was completely ice-free (Streveler and Paige 1971).

The cove has an area of 715 m^2, and is connected by a winding gut (channel), with gravel beach on the south and sheer granitic cliff to the north, to Muir Inlet. A sheer rock face bounds the cove on the north, a flat gravel beach to the east and south. Small numbers of icebergs arrive in the cove with each daily tide; the constricted entrance protects the water from the injection of large bergs, or large numbers of bergs. These bergs are often stranded on its shores when the tide falls.

A high granitic dome rises above the cliffs north of the cove. A similar dome west of this constitutes Sealer's Island, 720 m^2, covered with krummholz and tundra. During early summer, this island is a nesting site for glaucous-winged gulls and Arctic terns. During June and July, when these birds are especially defensive, feeding otters move over the entire surface of the island, including the summit. In August, when the birds had left, and the king crabs in the adjacent waters had moved to greater depths, the otters also abandoned the island. There was no evidence that the otters fed on birds.

The torrential outflow of glacial melt from the soles of tidewater glaciers in Muir Inlet north of Goose Cove, and the continual melting of icebergs, provides a freshwater lens over the waters of the cove, but its thickness is not determined. The water of Goose Cove is less turbid than that of Nunatak Cove, to the north, which is about as turbid as Thistle Cove. NPS ranger Dave Mills discovered, during dives in Goose Cove in 1978, that there is

a layer of clear water, 2 m deep, over the bottom of the cove.

Except during rains, there is no freshwater run-off into Goose Cove. An intermittent channel to the east of the cove leads down from some tundra ponds on the saddle between Goose and Nunatak Coves. The ponds are shallow (less than 1 m deep). The channel is usually dry.

In summer, 1977, NPS biologist Leigh Smith found otter sign around these saddle ponds, 0.75 km from the cove. In 1978, I found the feeding and rest sites Smith had identified the previous year torn up and trampled by moose. I found no sign of otter activity anywhere in that inland area in 1978.

Goose Cove was first noticed historically in 1936. A party of Tlinkit seal-hunters from Hoonah left a woman and child in the cove, and proceeded to Sealer's Island to hunt. When the hunters returned the woman and child had disappeared without a trace (Black 1956). Although this disappearance was attributed to the kushta-kah, or otter-man, this does not indicate otter presence at the time. The kushta-kah is a monster of human appearance, and may be active anywhere in the Tlinkit world, at any time (De Laguna 1972).

The first NPS summer ranger station was established at Goose Cove in 1965, and found otters already resident there. At the time the vegetation consisted only of Dryas and scrub alder less than 12 cm high. The camp has coexisted with the otters since that time.

From 1965 to 1970, the ranger camp consisted of tent-frames located on shore, 50 m from the water's edge, south of the cove. The ledges and rocks habitually used by the otters are on the north side.

In 1970, this tent camp was demolished by a brown bear. From 1971 to the present, the ranger camp has consisted of three floating platforms in the cove. The otters are active daily in the waters to within a few meters of these platforms. No otter has been known to climb up on one of them. Only the entry of the patrol boat into the cove displaces the otters from the water, and that only for so long as the motor is running.

Postglacial succession changes the vegetation, invertebrate, and vertebrate fauna to some degree annually. Octopus, tanner crabs, and Dolly Varden occur in Goose Cove all summer. King crabs move into the cove in moulting season, June and July, but are more common then on the shelf between the mainland and Sealer's Island. All of upper Muir Inlet is evidently a moulting ground for the local population of crabs, as is Adams Inlet. These crabs move into deeper waters after early August and are no longer found in otter feeding sites.

Dungeness crabs are rarely encountered at any time during the year.

Pink shrimp (Pandalus borealis) are the commonest of crustaceans in all Muir Inlet, and occur in Goose Cove throughout the summer. These shrimp are numerous at the faces of tidewater

glaciers. The calving of bergs, or the overturning of floating bergs, is an event which attracts seals kittiwakes, and other shrimp-eaters into the waters disturbed, because of the circulation of shrimp in the water. These effects are observed at the faces of glaciers.

I discovered echinoids on the shores south of Goose Cove, and on Sealer's Island, for the first time in summer, 1978. I had not previously observed echinoids farther north than the mouth of Adams Inlet. NPS rangers Dave Mills and Rick Caulfield, resident in Goose Cove for three years previously, confirmed that none had been seen at these localities until that summer.

In the early 1970's, mammal sign was common everywhere on the coast of Goose Cove and Muir Inlet. Human intrusion was negligible. Tracks of moose, brown bears wolverine, wolves, and coyotes were found on sand and gravel beaches daily. Mountain goats occasionally ventured near shore. In the late 1970's, human intrusion was widespread and frequent. Evidence for terrestrial mammal activity had declined sharply. Moose, coyote, and wolverine and sign was found much less frequently. Brown bears appeared to have abandoned the area.

Even the frequency of sightings of marine mammals had declined enormously. Harbour seals had previously been abundant in Muir Inlet. Over 1,000 seal pups were born each June on the pack ice at the face of Muir Glacier. Seals remained on ice floes by the hundreds, throughout the summer (Home 1973). In 1978, only single, widely dispersed seals were sighted after the pupping

season ended. Minke, humpback, and killer whales formerly entered Muir Inlet so far as to be visible from the mouth of Goose Cove. I saw none of these in 1978.

Despite these faunal changes, NPS ranger logs for Goose Cove from 1965 to present indicate that the activities, sites, and pod range of the Goose pod have not changed in any particular during this time.

Nunatak Cove, the next inlet north of Goose Cove, has been clear of ice since 1936 (Streveler and Paige 1971). Most of the water from the saddle ponds between Goose and Nunatak Coves drains into Nunatak Cove, and there is also a river charged heavily with glacial silt which empties into the cove.

Nunatak Cove has a wide mouth into Muir Inlet, and as a result, receives a considerable influx of icebergs and glacial silt. Mud flats, almost depauperate, cover half of the area of the cove exposed at low tide.

From 1967 to 1969, the ground cover in Nunatak consisted only of Dryas mats and alder seedlings. There was a resident otter pod at that time. Miners also lived on the beach, and reported activities of the otters in the cove and along the river.

No miners have lived there since 1971, and there have been no further records of otters in the area. A summer-long resident in 1978 confirmed that otters neither resided in, nor visited, the cove at that time (A. Milner, Chelsea College, London, U.K., pers. comm.).

The Goose pod is active in the gut between the cove and Muir Inlet, in the waters between the mainland and Sealer's Island, and on the surface of Sealer's Island, chiefly in June and July. In August, the cove itself is the only water in which the female and kits are active.

The male travels along the gravel beach to the south of Goose Cove, and the southernmost of the infrequent signs of random feeding which I located was 4.8 km south of the cove. No otter made any inland forays during summer, 1978.

The distribution of feeding sign around the shores of Sealer's Island indicates that otters do fish in the deeper waters north and west of the island. The pod's activity seems to be confined by the 18.75 m bottom contour, a depth accessible to diving otters (Scheffer 1953). Because of the steep gradient from the north and west cliffs of the island to the sea bottom, it is unlikely that otters fish far from shore on these sides, as they prey only on king crabs, which must be taken from the bottom.

Inside Goose Cove, the pod's activity is confined to the waters of the cove and gut, and the cliffs on the north side to an elevation of 6 m above mean water line. There is no den, but a habitual resting ledge seems to serve its purpose. The otters apparently come ashore on the south side only rarely, and at night (IV.2. below). Random feeding remains are never left on the gravel beaches inside the cove. All feeding sign is to be found on the resting ledge and nearby rocks. There are no altars as such (III.3, below).

In summer, the total water area exploited amounts to 1.9 km^2. The total land area exploited by the male, considering the surface of Sealer's Island, the thin zone along the shore, and the beaches to the south of the cove, is less than 1 km^2. The total linear coastline on which evidence of the pod is found amounts to 8 km, but the female and kits are active on only 2.7 km of this.

The female and kits are active over most, if not all, the surface of Sealer's Island, but rarely go ashore elsewhere. Their total land area usage is thus 0.75 km^2.

In August, 80% of the observed activity of the pod was confined to about 20% of this entire range - the focal water and its shores. This total range is much smaller than that of any other pod. The Goose male may have been alone in penetrating the saddle ponds in 1977. As he did not hunt voles in the summer of 1978, when vole populations were at highs inland and around the cove, it is unlikely that this male ever penetrated inland.

Opposite Goose Cove, the Rowlee pod, utilising the same type of shoreline, operates over a much wider areal range. This may be due to the fact that the Rowlee pod has no enclosed, protected focal water in which prey are concentrated with little competition from other foragers.

I sighted the male of this pod 11.3 km north of Rowlee Point, in Wachusett Inlet. The pod is also active south to Point McLeod, 2.6 km south of Rowlee Point, and perhaps around

the shore of Hunter's Cove. The linear coastline exploited by the male of this pod is at least 19.3 km, the longest of any individual studied. The barrenness of the country inland from this coast suggests little likelihood that any of these otters go inland in any season.

F. Features of Pod Ranges

Despite the absence of scat-marked boundaries, or of internecine conflicts, the concept of territory is appropriate to the range included within the habitat exploited by a given otter pod on the shores of Alaska. Otters do respond to removal of, or interference with, their scat deposits on prominent or habitual sites, even though they show no other response to human intrusion in such areas.

Along the Pacific coast, otter ranges are defined in reference to a specific body of water. A single pod's range may include a river, streams, a lake, and a marine bay, all of which are used to some extent on an annual, or even weekly, basis. Only one of them may be described as the "focal water," characterised by repeated, consistent, and usually daily foraging activity. There appears to be only one focal water in any pod's range, although seasonal events, such as fish runs may concnetrate the pod's activities elsewhere for weeks at a time.

On the Pacific coast, the ratio of one pod per fjord seems a matter of adaptive convenience. Each pod there is exploiting the existing resources to a maximum. This is supported by the fact

that the number of scats collected there in winter is substantially less than those collected in summer (Streveler 1977), and that the total number of scats collected around the year is less than the number of scats collected over the same periods for pods within Glacier Bay. It is also in keeping with the marginal nature of this range, as exhibited by other species (Home 1977).

Pods are distributed along the Pacific coast at the ratio of 1 pod/fjord, inlet, or bay, regardless of the length of the shore or character of the inland range. The terrain of these inlets differs sharply from one to the other. Accordingly, so do the habits and activity patterns of the otters exploiting them.

These fjords are demarcated from each other by reefs, promontories, and other features exposed to swell, winds, and storm. Otters have no reason to go around these promontories, and I have no evidence that visits are made even to the oceanward extremes of these fjords on any occasion, even by solitary males.

The geological features which separate the fjords are also those which separate the inland ranges behind the fjords. Otters are well able to climb the most difficult cliffs, and do so for indeterminable reasons. Even when they do so, I find no evidence of contact between two pods in an inland range.

Inside Glacier Bay, coves and inlets are less sharply separated by geological features, and the coast is less irregular. Small coves or other well-defined salt water areas constitute focal waters, but so do restricted areas in an open bay. Away from these

focal waters, exploitation of the coast seems to be so random and infrequent as to suggest that the food resources within the focal waters are sufficient for the pod, even at a low minimum. Any one pod feels less pressure to exploit a diversity of range features, unless its focal water has no reliable stock of prey (such as the Boussole pod).

In Muir Inlet, discontinuities between pods are marked by sheer sea cliffs, or by flat gravel beaches, without any obvious partitions. Here, as in other parts of Glacier Bay (e.g. Adams Inlet) there may be no truly enclosed waters, or usable freshwater flows. These periglacial ranges are more barren in terms of terrestrial resources and vegetative cover than any other part of Glacier Bay and the otters resident there are oriented more strictly toward marine resources in foraging.

Large amounts of feeding sign are concentrated at habitual eating sites in Muir Inlet, and there is less evidence of random feeding sites anywhere. In Goose Cove, this concentration is concomitant with a greater degree of association between the male and the rest of the pod. This fact itself might be due to the proximity of human activity, but similar concentrations and evidence exist at three other focal waters within Muir Inlet.

A given area of the open inlet may be recognised by a pod as its focal water when concentrations of feeding remains, particularly "chancels" (III.3, below) are located at the shore. Limits may be recognised in such areas in reference to shallow bottom,

where food sources tend to be concentrated within easy access. King crabs must move into very shallow water at the mouth of Adams Inlet in order to leave the inlet, and enter the deeper waters of Muir Inlet, after moulting. It is that point at which the inlet is the most shallow that the Adams Inlet pod deposits great amounts of feeding remains, consisting chiefly of king crab fragments.

Pods which have access to rivers and lakes are about equally active along these watercourses as along the seashore, if the rivers support prey populations. The river which enters Adams Inlet is so charged with silt that neither fish nor plankton can survive in it, and even the banks are devoid of life. There is never any sign of otter activity along this river.

Possibly the differential use of the saddle ponds inland from Goose Cove is due to the frequency of water flow through the connecting channel. The otters may follow this flow to the ponds only when there is water running. When the channel is dry, as it was in 1978, the otters may not attempt to go to the ponds.

The case of Nunatak Cove shows that not all possible or potential ranges are exploited, at least not indefinitely. The reason for this is unknown. There is a high incidence of population turnover of the otters in Goose Cove, the nearest neighbour (IV.2, below). Population in periglacial ranges may be more unstable than those elsewhere; predation may be a factor (V.1, below).

There is no apparent relationship between the actual size of bodies of water and the intensity of use by the resident pod.

The Goose pod spends more of its time, daily, in Goose Cove than the Thistle pod spends in Thistle Cove. Thistle Cove is ten times the size of Goose Cove, but Goose Cove may have several times the available biomass of prey that Thistle Cove supports, relative to the otters alone.

The focal water for both the Thistle and Goose pods is a saltwater cove. The Barco pod's focal water is a saltwater lagoon and part of a sea channel. The Boussole pod's focal water is a river and slough system. The focal water of the Gustavus pod is a river, with no use of a marine zone (Table 3 lists focal waters for several other pods).

The Goose pod is the only otter pod studied which makes no use of any freshwater flow.

A pod's range beyond the focal and associated waters is variable. It does not necessarily depend on the terrain, or other ecological features of the range. The Boussole pod ranges over river, sloughs, sea beach, forest floor, escarpment cliffs, and ponds. The adjoining Thistle pod has access to all of these features, but ranges through them to a much reduced degree. The difference reflects the availability of food in the focal water.

The range of the female and kits is 1/3 that of the male in two of the four pods studied, and is indicated for a third (the Goose). This ratio is therefore the same despite the fact that the basic foraging modes and ecological strategies of the three pods are different.

Land foraging and other activity is minimal for the female and kits, relative to the male. In focal waters, the activities of female/kits and male overlap. In peripheral parts of the range, the male is generally alone. In the Boussole pod, the female sometimes accompanied the male into peripheral territory.

Gravel sea beaches are preferred activity sites for all otters (Table 3). Sand beaches are sometimes crossed or hunted, but, except on unusual occasions, such as the deposition of benthic organisms over the sand of Boussole beach, otters avoid sand and especially muddy beaches. Gravel beaches, rock faces, and talus are optimal otter range. Sand and mud beaches are not optimal range at any time.

Rock features are associated with most kushta otters. There are, however, no boulders, rock cliffs, faces, or altars in the Barco pod's focal water, although there are boulders and talus in other parts of its range. Cavities and declivities in rocks are sometimes selected for dens. Summits of sarsens are preferred as feeding sites (III.3, below). When dens are not used, there is still an orientation to rock faces or boulders, as evidenced by the Goose pod's use of resting ledges.

Even if there is no den, vegetational concealment is not required by otters. The Goose pod was resident in Goose Cove at least five years before the ground cover was as much as one meter high, and could offer any concealment. Most of the area around Rowlee Point is still deficient in such tall vegetation.

There is no evidence of any preference for a specific vegetational or forest type by otters. Otters move over the forest floor in spruce-hemlock, alder, or pine forest equally, depending on the access to watercourses. Otters usually occupy dens in the roots of trees, because they do not dig their own dens (Liers 1951), and make use of what they can find. Dens are not located in rock only, although rock dens are used when available.

The dens I have studied have been located within forest cover over a base of morainal gravel. None provide any protection from predators. A den near Lake Andromeda, in the Boussole Valley. was located in the roots of a spruce, directly on a trail used by wolves and bears.

Dens then occur in random locations throughout a pod's range. Not all usable formations may be occupied. Use of dens themselves is discontinuous. In some cases, dens are used only seasonally, as in association with fish runs in rivers. The otters I have observed may occupy the same den or retreat continually for months.

Occasional one-time use is made of temporary refuges, probably by the male alone, for sleeping. One winter night in Thistle Cove a single adult went ashore on the sandy east shore, otherwise never visited by the otters. This otter crawled into a shelter formed by two isolated rocks and compacted the snow sufficiently to indicate it had rested there for some time.

There is at present no visible relationship between the size of a pod's range and the number of dens therein.

In my observation, kushta otters do not make trails, as inland pods do (Seton 1910, Liers 1951). Watercourses are the main channels of movement. Overland activities do not follow repeated routes, other than to den entrances or altars.

Even specific escape routes, a characteristic of each focal water and altar, do not follow worn trails. These routes may lead only to a place of concealment in the vegetational cover, and not to any real refuge. Use of such retreats is a constant during alarm displacements.

The male does much of its wandering at night, and is seen with the rest of the pod more often in the daytime than he is absent from it. When the total area covered by the wanderings of the solitary male is considered, pod ranges are large.

Together with the evidence provided by the food habits of three of these pods (III.3, below), observations of the activity within pod ranges supports the following conclusions as to three separate ecological strategies exhibited by kushta otters.

(1) The Boussole pod, relying largely on a river-slough system with minimal, but regular, sea foraging, depends on a large overland territory despite a low food yield therein. This can be styled the "supermink" strategy. This mode has points in common with the strategies of inland otters, especially those which exploit marginal ranges. Like a Michigan pod in winter described by

Field (1970), the Boussole pod has no regular or established eating sites, but leaves feeding sign at random locations along its winter trails, or, during salmonid runs, along the river banks.

This "supermink" pod exhibits more dissociation of pod members than the others; sometimes both adults leave the kits. (In inland Swedish pods, families also sometimes dissociated ((Erlinge 1968))). The male makes prodigious cliff climbs, although other marine-oriented otters exhibit the trait. The determination to surmount cliffs in winter to check areas which yield food resources only in summer is so consistent, that it appears that this strategy is equally dependent on each substrate feature to a degree which allows no substitution of one on the failure of another; these otters are unable to dispense with any part of their especially eurytopic range.

Biochronologically, the "supermink" strategy is probably the oldest and most primitive otter habitus.

Both the Thistle and Barco pods exhibit the intermediate "roensis" strategy. The foraging behaviour utilised by this pod does not rely on any facultative thigmotter performance, since little energy is expended in collecting urchins or other bottom fauna; crabs are brought up orally (III.2, below).

The Thistle pod experiences little pressure to maximise its foraging in freshwater and overland ranges, because of its fortunate location at a marine focal water with food resources adequate for the pod (as well as for numerous other predators). The

Barco pod has the same good fortune with even less competition; perhaps predators here are deflected by the human presence which does not annoy otters, and the otters are thereby benefitting from the human occupancy in a rare, genuine instance of commensalism.

When terrestrial food resources are available, the male of the Thistle pod makes use of them. When such food resources dwindle, the pod is able to obtain sufficient forage from the focal water. Presumably, if marine resources were to drop (there is evidence that this occurs at times, Home 1977) the otters would still be able to maximise activities overland and upriver to compensate; some forage can be obtained there at any season, though at a greater expenditure of energy per individual.

The "roensis" strategy includes the use of dens, many used only intermittently, or abandoned for long periods, but some of them are used intensively for years at a time. Regular feeding sites, such as middens and altars (III.3, below), are a character of "roensis" pods. Pod association is more consistent, on a daily and year-round basis, than is observed for the "supermink" mode. This consistency may be less than for the "phocoid" strategy, and intermediate between the two. The "roensis" otters spend far more time immersed in water than do the "supermink" otters.

The Goose pod, oriented almost exclusively to marine resources, and making little use of land except for resting and feeding sites (except for one gigantic altar, III.3, below), represents a stage in the evolutionary ecology of otters having more

in common with sea otters and, ultimately, with seals. Readily available terrestrial foods are not taken (III,1, below). There are no dens, at least in summer. Interassociation of the pod seems more regular both day and night. The male explores the coastline, but makes no inland forays for entire seasons.

This can be called the "phocoid" strategy. It is the most likely to be selected for in environments originally occupied by the otters when almost deficient of vegetative ground cover and resident terrestrial prey. It would also be characteristic of otters occupying desolate coasts, not biochronologically recent, such as those of northern Scotland (Elmhirst 1938). Such environments do tend to produce "almost wholly marine animals."

G. Summary

Cliffs can be climbed. Slopes can be surmounted. Neither icebergs, jötulhlaupir, nor barren flats stay these otters from completion of their determined rounds. However violent the swells, currents, or breakers, all water is transport to otters, not barrier. Only mountains or the surfaces of glaciers themselves put decisive limits on otter activity.

From the depths of the whales to the heights of the goats, and the oldest forests to the faces of active glaciers, the otters exhibit a broader ecological amplitude than that of any other species in Glacier Bay, or any other part of southeastern

Alaska. In this lies the key to their widespread distribution and adaptability to all areas, whatever the topographic character.

It is evident that otters are less dependent upon the geological or biochronological stade of a given terrain than are other mammals which succeed to deglaciated range. Otters are able to maintain specific foraging and life history strategies indefinitely in a variety of terrains and sea types as long as any one of the preferred foods is in adequate supply, without regard to changes which may occur in the environment around them.

There is evidence of a degree of conservatism in the pod range and in the pod's activities, but this does not influence in an unbalanced way the pod's ability to adapt to a variety of resources, and make alternate use of several resource bases, as required.

The adaptive requirements which, in the past. have shaped a great variety of species into greater specialisations - the polecat, mink, "supermink," thigmotter, trichotter, and finally phocid - are exercised today at the same time, and nearly the same place, but a single species which persists largely because of its ability to produce any of these responses to adaptive requirements from a generalised, primitive, conservative somatic and behavioural base.

Otters are clearly not affected by non-destructive human activities. Otters coexist with human beings here and elsewhere

with less change of their habitual activity patterns than those shown by any other species.

Otters occupy the same sites from year to year, regardless of the change of circumstances (or succession in the ecology). At the same time, their offspring remain capable of colonising environments without precedent in the experience of any individual otter.

III. LUTRINE GASTRONOMY AND NUTRITION

III.1. CHOICE OF PREY

A. Methods

For the methods employed in collecting the data analysed in this section, refer to I.1.B, above.

B. Literature

A simple statement sums the entire literature on the feeding habits of L. canadensis and L. lutra anywhere in the world: anything that can be eaten, will be eaten. But local populations show distinct preferences among locally available prey.

On an annual basis, the diversity of otter foods is greater than the diversity of foods chosen in any one season. The greatest range in the species diversity of prey taken by single pods (or individuals) occurs among inland otters (Table 8 gives data from Greer 1955, Hamilton 1961, etc.). Among inland otters, individual scats routinely contain a variety of food materials, reflecting diversity in prey and foraging strategies during the preceding hour (Liers 1951).

Among kushta otters, by contrast, it is less usual for one scat to contain more than one prey component, and when other

items are present, such items are often so small in size or slight in significance as to be have been taken incidentally to the pursuit of the dominant food item. The frequency of occurrence of the same prey in many scats is high for all kushta otters (Grinnell et al. 1967); Foottit and Butler 1977; Hatler, pers. comm.) as is illustrated in Tables 6 through 13.

Tables 8 through 12 sum reports from the literature. Tables 5 through 7 and 13 report my own studies, for comparison.

Table 8 lists reports of prey incidence in scats and stomach contents of inland otters from Massachusetts, Michigan, and Montana. Similar studies of the foods of inland L. lutra in Britain reveal the same frequencies and patterns (Stephens 1957). Table 9 lists reports from British investigators, identifying the foods of seagoing otters from the coasts of Cornwall, Ireland, and Scotland. Table 10 lists what slight data is available for the Arctic kushta otters of the Kola peninsula and Kil'din Islands (Formozov 1927, in Ognev 1972). Table 10 shows that little is known of the feeding habits of the chungungo, the sub-Antarctic kushta species. Table 11 lists foods identified in the scats of kushta otters reported from British Columbia, Washington, and California; this data is non-quantitative because it is so limited in scope.

Table 12 lists foods identified as taken by sea otters in California and Amchitka Island.

TABLE 4. ALL SPECIES OF ANIMALS PREYED UPON BY KUSHTA OTTERS THROUGHOUT SOUTHEASTERN ALASKA

Sources: Author's observations, and original reports cited herein

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I. MOLLUSCA

1. Amphineura
   Chitons (sp. indet.)

2. Gastropoda
   Limpet (Acmaea digitalis)
   Snail eggs (Thais sp.)

3. Bivalvia
   Edible blue mussel (Mytilus californianus)
   Steamer clam (Mya arenaria)

4. Cephalopoda
   Octopus sp.

II. ARTHROPODA (CRUSTACEA: MALACOSTRACA)

1. Amphipoda
   Gammarid spp.
   Caprellid spp.

2. Isopoda
   Exosphaeroma

3. Decapoda
   Pink shrimp (Pandalus borealis)
   Dungeness crab (Cancer magister)
   King crab (Paralithodes camschatica)
   Tanner crab (Chionoecetes bairdi)

III. ECHINODERMATA

1. Echinoidea
   Strongylocentrotus droebachiensis

IV. VERTEBRATA

1. Chondrichthyes
   Skate (Raja binoculata)

2. Osteichthyes
   Gadidae: Pacific cod (Gadus macrorhynchus)

(Continued

TABLE 4. (Continued)

Clupeidae:	Herring (*Clupea harengus*)
Salmonidae:	Dolly Varden (*Salvelinus malma*)
	Red salmon (*Oncorhynchus nerka*)
	Chum salmon (*O. keta*)
	Coho salmon (*O. kisutch*)
	Humpback salmon (*O. gorbuscha*)
	?Steelhead (*Salmo gairdnerii*)
Osmeridae:	Eulachon (*Thaleichthys pacificus*)
	Capelin (*Mallotus villosus*)
Pleuronectidae:	Halibut (*Hippoglossus stenolepis*)
	Starry flounder (*Platichthys stellatus*)
Cottidae:	Staghorn sculpin (*Leptocottus armatus*)
	?*Cottus aleuticus*
	Irish lord (*Hemilepidotus hemilepidotus*)
	Bullhead (*Scorpaenichthys marmoratus*)
Gasterosteidae:	Threespine stickleback (*Gasterosteus aculeatus*)
Pholidae:	Gunnels (*Pholus* spp.)

3. Amphibia
   ?Boreal toad (*Bufo boreas*)

4. Aves
   Common goldeneye (*Bucephala clangula*)
   Bufflehead (*Bucephala albeola*)
   White-winged scoter (*Melanitta deglandi*)
   Glaucous-winged gull (*Larus glaucescens*)
   Common murre (*Uria aalge*)
   Pigeon guillemot (*Cepphus columba*)
   Murrelet sp. indet. (*Brachyrhamphus* sp.)
   Red-breasted merganser (*Mergus serrator*)
   Mallard (*Anas platyrhynchos*)

5. Mammalia
   Shrew (*Sorex* sp. indet.)
   Vole spp. (*Microtus oeconomus*, *M. longicaudus*, *Clethrionomys rutilus*)
   Northern sea lion (*Eumetopias jubatus*)

TABLE 5. PREY IDENTIFIED FROM OTTER SCATS AND FEEDING REMAINS IN SOUTHEASTERN ALASKA SITES NOT INTENSIVELY STUDIED, 1967-1978

BARTLETT COVE (Streveler, unpublished data; Home 1973)

Chitons (sp. indet.)
Octopus sp.
Amphipods sp. indet.
Pandalid shrimp (either Pandalus borealis, P. dispar, or both)
Dungeness crab (predominant single item in all years and seasons)
Tanner crab
Sea urchin
Threespine sticklebacks (predominant osteichthyan prey)
Skate, Raja binoculata
Goldeneye
Bufflehead
Red-breasted merganser

REID INLET (Streveler, unpublished data, 1967-1973)

Pillbug, Exosphaeroma oregonensis
Pink shrimp, Pandalus borealis
Threespine sticklebacks
Unidentified small fish
Unidentified bird

SITKA HARBOUR (Scheffer 1953)

Bullheads
Clams (sp. indet.)

INDIAN POINT (Home, herein)

Halibut

ETOLIN ISLAND (Home, herein)

Humpback salmon

TAIYA RIVER (Home, herein)

Chum salmon

BROWNSON ISLAND (Home, herein)

Echinoid spp. (predominant item)
Dungeness crabs
Sticklebacks

TABLE 6. FOODS OF THE THISTLE AND BOUSSOLE PODS

1. THISTLE POD: Feeding Remains, Winters 1973-75 (Home 1977)

Prey	Individuals in feeding remains
Dungeness crab	54
Dolly Vardens	16
Unidentified salmonids	12
Unidentified fish (prob. cottid)	3
Pacific cod	1
Murrelet sp.	1
Common murre	1
Glaucous-winged gull (immature)	9

2. THISTLE POD: Scat Contents, Summer 1975 (Streveler 1977)

Prey	Volumetric Assay[1]
Isopods, other small crustaceans	3.4%
Cancer magister	56.2%
Salmonid fish	35.2%
Non-salmonid small fish	5.2%

3. THISTLE POD: Feeding Remains, Summer 1975 (Streveler 1977)

Prey	Individuals in feeding remains
Dungeness crabs	21
Gull sp. indet.	1

[1]Streveler's percentages represent the total volume of the item identified from all otter scats retrieved from Thistle Cove and Torch Bay - two separate otter pods - in summer, 1974. His tables do not indicate the distribution of foods between the two pods.

(Continued

TABLE 6. (Continued)

4. THISTLE POD: Scat Contents, Summer 1974 (Streveler 1975)

Prey	Volumetric Assay
Snail eggs (Thais sp.)	0.3%
Mussels and clams	0.5%
Amphipods	2.6%
Isopods (Exosphaeroma)	0.3%
Cancer magister and other crabs	3.7%
Salmonid fish	77.4%
Non-salmonid fish	12.9%
Murrelet sp. indet.	2.6%
Shrew sp. indet.	0.3%

5. BOUSSOLE POD: Feeding Sign and Remains, Winters, 1973-75 (Home 1977)

Prey	Individuals in Feeding Remains
Sculpins	5
Sticklebacks	3
Guillemots	2*
Common murre	2*
Glaucous-winged gull	4*
Sea lion	1*

* Scavenge items

6. BOUSSOLE POD: Feeding Sign and Remains, Summer and September, 1975 (Streveler 1977)

Prey	Volumetric Assay
Red salmon	100% (30 scats)

TABLE 7. FOODS OF OTTERS IN MUIR INLET, SUMMER, 1978

Prey Item	No. of Scats/Remains	%age Total
I. GOOSE POD		
1. Sealer's Island, Scat and Feeding Remains, June and July Feeding		
Mussel	7	7.7%
Pink shrimp	12	13.2%
King crab	43	47.3%
Echinoids	6	6.6%
Fish (80% Dolly Varden, remainder unidentified)	23	25.3%
Bird, unid.	1	0.9%
	91	100.0%
Overlap (incidence of two materials in the same scat) = 2.2% (e.g., 1 scat: fish and crab; 1 scat: crab and bird feathers)		
2. Goose Cove, Scat and Feeding Remains, August Feeding		
Mussels	3	5.3%
Pink shrimp	48	84.2%
King crab	2	3.5%
Dungeness crab	3	5.3%
Echinoids	2	4.1%
Bird (?goose)	1	1.8%
	59	100.0%
II. ROWLEE POINT POD		
1. Rowlee Point, Scat and Feeding Remains (June, July, August Feeding)		
Mussels and limpets	1	0.6%
Pink shrimp	33	20.8%
King crab	68	42.8%
Fish (Dolly Vardens, unid. smaller fish)	52	32.7%
Bird (unid.)	5	3.1%
	159	100.0%
Overlap = 1.8% of scats (1 scat: mussels and limpets; 1 scats: crab and birds; 1 scat: crab and birds)		

(Continued

TABLE 7. (Continued)

2. Wachusett Inlet, North Entry. Scat and Feeding Remains, July and August Feeding

Mussel[1]	5	27.7%
King crab	7	38.9%
Tanner crab	2	11.1%
Dolly Varden	3	16.7%
Pigeon guillemot	1	5.6%
	18	100.0%

[1]Deposit of mussel shell shards on bank, not associated with scats

III. ADAMS INLET POD

1. North Entry, Adams Inlet (A deposit censused 25 August 1978)

Mussels	21	20.8%
Pink shrimp	14	13.9%
Crabs[1]	44	43.6%
Echinoids	2	2.2%
Fish (80% salmonid, remainder prob. cottid)	18	17.8%
Bird (unid.)	4	4.0%
	103	100.0%

(Continued

TABLE 7. (Continued)

IV. TOTAL of All Foods in Scat and Feeding Remains for Muir Inlet Otter Pods, Summer, 1978

Prey	Scat Numbers	Subtotal	Total %age
Limpets	1		0.2%
Mussels	32		7.8%
Pink shrimp	107		26.0%
King crabs	153	37.2%	
Dungeness crabs	3	0.7%	
Tanner crabs	2	0.5%	
Total crabs			38.4%
Echinoids	12		3.6%
Fish (80% Dolly Varden)	93		22.6%
Birds (ducks/gulls/ guillemots)	11		2.7%
Total	430		100.0%

Total overlap: 0.9%

TABLE 8. FOODS TAKEN BY INLAND POPULATIONS OF RIVER OTTERS

Sources: Selected studies as cited

Prey	Percentage in Scats				
	Winter	Spring	Summer	Fall	Total
1. Montana, Scat Analysis (Greer 1955)					
Crayfish, aquatic insects (8 spp)	26.3%	41.6%	44.2%	33.3%	41.2%
Fish (10 spp)	100.0%	91.4%	92.9%	100.0%	93.2%
Amphibians (2 spp)	9.1%	19.6%	19.5%	12.0%	18.4%
Reptiles (1 sp)		0.2%	0.7%		0.4%
Birds (2 spp)	5.1%	6.7%	4.1%	1.3%	5.2%
Mammals (7 spp)	2.0%	8.1%	5.3%	2.7%	6.1%
2. Michigan, Stomach Contents (Lagler and Ostenson 1942)					
Crayfish		35.0%			
Insects, larvae		4.2%			
Fish		52.0%			
Amphibians		16.0%			
Reptiles, birds, mammals		25.0%			
3. New York, Stomach Contents (Hamilton 1961)					
Crayfish					35.0%
Fish					70.0%
Amphibians					35.0%
Insects, mammals, birds					traces
4. Massachusetts, Stomach Contents (Sheldon and Toll 1964)					
Crayfish					56.0%
Insects					trace
Fish					92.0%
Birds					1.0%
Mammals					3.0%
Vegetation (blueberries)					13.0%

(Continued

TABLE 8. (Continued)

	Spring
5. Michigan, Stomach Contents (Ryder 1954, 1955)	
Insects and larvae	13.0%
Centrarchids	40.7%
Trout	13.0%
Sticklebacks, mudminnows, minnows	55.5%
Amphibians	16.7%
Spiders, pelecypods	traces

TABLE 9. PREY OF KUSHTA OTTERS OF SCOTLAND, IRELAND, CORNWALL, AND ENGLAND

Sources: As cited

Locality	Author	Fish	Crustaceans	Other
Scotland	St. John (1846)	Flounders	Crabs	Rabbits Hares
Scotland	T.J. (1886)	Salmon		
Scotland	Harvie-Brown and Buckley (1892)	Salmon Sea-trout		
Scotland	Elmhirst (1938)		*Idotea granulosa* (taken in sea) *Gammarus duebeni* (in tidepools) *Orchestia littorea*, *Porcellio scaber*, *Ligia oceanica* { above drift line *Carcinus maenas* (predom. in scats, highest in littoral zone) *Cancer pagurus* (intertidal) / *Portunus puber* (lowest)	
Ireland	Ogilby (1834)	Salmon		
Cornwall	Tregarthen (1929)	Conger eels		
British coasts	Harrison Matthews (1952)	Flatfish Wrasse Cod, other gadids	Crabs Crustacea "as small as sandhoppers"	

TABLE 10. PREY OF ARCTIC AND SUB-ANTARCTIC KUSHTA OTTERS

Source	Crustaceans	Fish	Other
1. Lutra lutra, Kola Peninsula (Formozov 1927, in Ognev 1972)	None given	93%	Snowshoe hares Voles Shrews Muskrats Sumpfotters
2. Lutra felina, Southern Pacific Coast of South America			
(Darwin, in Waterhouse 1839)	"red prawn-sized crab of the Macruri" "large spiny crab, Lithodes antartica"		Volutes Cuttlefish
(Coppinger 1883)	spiny crab (principal food)		
(Simon 1966)	freshwater prawn, Criphiops caementarius (principal food)	Fish	Shellfish
(Martin 1977)	freshwater prawn, Criphiops caementarius (principal food)		

TABLE 11. PREY OF KUSHTA OTTERS ON THE WEST COAST, NORTH AMERICA

Locality	Source	Crustacea	Fish	Others
Humboldt County, California	Grinnell et al. 1937	Crayfish, 100%	Unid. fish	
British Columbia coast	Foottit and Butler 1977			Gull chicks
	Verbeek and Morgan 1978			Gull chicks (82%, August)
	Hatler, pers. comm.	Helmet crabs, 25% Crayfish, 100% "at times"	Fish, 75%[1]	
Colville Island, Washington	Hayward et al. 1975			Gull chicks and adults

[1] Species include the cabezon (Scorpaenichthys marmoratus), lingcod (Ophiodon elongatus), starry flounder (Platichthys stellatus), red Irish lord (Hemilepidotus hemilepidotus), wolf-eel (Anarrichthys ocellatus), rockfish (Sebastodes sp.), gunnels (Pholus spp.), and sticklebacks (Gasterosteus spp.).

TABLE 12. PREY OF THE SEA OTTER (Enhydra lutris)

I. California sea otters (Shimek and Monk 1977)

Abalones
Turbine snails
Moon snails
Mussels
Octopus, squids
Annelids
Echiurids
Crabs (kelp crabs, gaper crabs)
Sea urchins
Ascidians

II. Aleutian sea otters (Kenyon 1969)

Prey	Percentage Incidence
Annelida	
3 spp., sandworm, ribbon worm, lugworm	2%
Crustacea	
Isopods, amphipods, shrimp, hermit crabs, *Cancer* sp., *Paralithodes* sp., shrimps	7%
Mollusca	
Amphineurans, gastropods (*Thais*, *Natica*, *Buccinum*, *Acmaea*); pelecypods; mussels, octopus	31%
Echinodermata	
Asteroids, brittle stars, echinoids, holothurians	37%
Tunicata	
2 spp	1%
Osteichthyes	
Sablefish, mackerel, Irish lord, globefish, etc.	22%

C. Comparison with Glacier Bay Studies

Comparison of these tables shows that the differences between seasonal and annual diets, in terms of choice and numbers of different species taken as prey, rather than in the volumetric intake of foods, is much less among kushta otters than among inland otters.

The point in common between both Holarctic species of otters, inland and kushta, is a dependence upon, and a preference for, crustaceans. Predation on insect larvae, when it occurs among inland otters, may compensate for the lower incidence of crustacean species in the waters inland otters exploit habitually. It may even be that this pursuit of insect larvae inspires eastern North American otters to eat berries. Insect larvae are found in most berries of Alaska, but I have no records of otters eating them here.

Liers (1951) found crayfish the preferred food of inland otters at any season of the year. Grinnell (et al. 1937) found the freshwater crayfish Astacus klamathensis in 100% of the otter scats in Humboldt County, California. The chungungo feeds principally on the prawn, Criphiops caementarius, and follows migrations of this species along the South American coasts (Simon 1966, Martin 1977).

In Glacier Bay, crabs and shrimp predominate in the otter diets both winter and summer. Crustaceans compose 64.4% of summer foods in Muir Inlet. On the Pacific coast, crustaceans

account for 59.8% of summer foods. Dungeness crabs are dominant in the winter food of the Pacific pods. There is no winter data for Muir Inlet.

The importance of fish in otter diets has been exaggerated. Quantitative studies of otter foods refute the contention that fish is the major food of otters. Liers (1951) discovered that otters fed exclusively on fish did not remain in good health. However, the differential biomass indicated by fish remains in otter scats, compared to the indigestible parts of crustaceans, indicate that large amounts of fish are never absent from otter diets, except for periods of time of a few days or a week.

This discussion will show that otters are not particularly good fishers. Inland otters are limited in their choice of prey to fishes which are not particularly good swimmers, but this is less true of kushta otters. Salmonids constitute 80% of the fish taken by kushta otters in Glacier Bay, and salmonids are efficient swimmers. In September, when salmonids are available in quantities in rivers and streams, otters feed on them almost to the exclusion of other prey, but the fish then are moribund, easy of access, often too crowded in narrow streams or pools to escape any predator however clumsy. At other times, fish are taken opportunistically in the pursuit of other prey.

Most otters feed occasionally on birds and mammals, especially in winter. But the incidence of bird and mammal food is

is much lower among kushta otters than among inland otters. Again, most such prey is taken incidentally to the pursuit of other prey, except for the "supermink" strategians, which exploit what is in nutritional terms a marginal situation.

It is significant that only a few otter pods in Alaska prey upon echinoderms, since echinoids are common foods of other otters, and of mink. Because of the low biomass yield per unit capture effort, this is probably a food which is abandoned whenever prey which provide a higher yield of biomass per unit capture effort are available. Perhaps echinoderm-dependent kushta otters are following a distinct, "thigmotter" ecological strategy.

D. Mollusca

1. Amphineura. In the 1960's, and occasionally in the early 1970's, remains of unidentified chitons were left on the Bartlett Cove dock by otters (Streveler's logs). Individual chitons in the Bartlett Cove lagoon sometimes reach large size, but no species of amphineuran is common in this region.

2. Gastropoda. Limpets (Acmaea digitalis), and eggs of the snail Thais sp., are among infrequent foods recorded for the Pacific coast (Table 5) and Barco (Table 6) pods. Both gastropods are common everywhere in Glacier Bay. Both are abundant along the Pacific coast.

I found one scat on the north shore of Wachusett Inlet composed half of limpets, and half of mussel shells. This is the

only record of limpets from Muir Inlet scats. I have no information on the abundance of limpets there.

Snail eggs have been found in scats on the Pacific coast in summer, only (Table 5). Both gastropods are unimportant, and probably incidental, foods.

3. Bivalvia. Mussels are said to be much relished by otters (Harris 1968). The edible blue mussel, Mytilus californianus, is common in large beds in all the subtidal, and many intertidal, zones along the shores of Glacier Bay, and on the Pacific coast. But mussels are fed on frequently only by the otters of Muir Inlet, where mussel beds are smaller and more widely dispersed.

This may be a result of the low faunal diversity of Muir Inlet. There seem to be few or no other bivalves in the gravels of the intertidal and subtidal zones in Muir Inlet, where mussel beds are exposed at low tides.

Partially broken mussel shells are found only rarely. Small, triangular shell fragments, no more than 0.75 cm at the widest point, occur in masses in some scats. These are the first scat contents which become loose, and which scatter from the dried mass of a scat. In old, dry scats, all these shell fragments have become loose, and litter the substrate without evidence of association with the rest of the scat. Such litters of triangular shards are thus invariable sign of otter feeding on mussels. No such regularity of fragments occurs in mussels broken by birds.

Cleaned, intact mussel shells are found on all beaches of Glacier Bay. These can not be assigned to otter predation without some positive sign of biting or breaking.

Shell fragments are most abundant in the scats left at the entry to Adams Inlet. Such fragments were found in lesser numbers in the Goose pod's scats on Sealer's Island (July feeding), the Rowlee pod's scats on Wachusetts Inlet and Rowlee Point (June and July feeding). The three Muir Inlet pods are thus active mussel-feeders, while the other pods are not.

These mussels become poisonous in late August and early autumn when they begin to ingest phosphorescent dinoflagellates. The toxin is strong, and is transmitted to consumers (Lutz 1980). Since human consumers die with stomachs full of mussels, the toxin evidently can not be detected by the chemical receptors. It seems unlikely that otters could be immune to it.

The female in Goose Cove was pulling mussels from a bed as late as 21 August 1978. No phosphorescence had appeared in the Muir Inlet waters by that date. In previous summers, the diagnostic phosphorescence was observed in lower Glacier Bay before that date.

There was, however, no evidence that mussels were being eaten in late August. This may have been a training exercise for the kits' benefit, but it is difficult to believe an otter would secure a food item and then leave it uneaten. Possibly there

a chemical reaction which warns the otters of unfit mussel flesh; possibly in the colder, ice-ridden waters of Muir Inlet the poisonous dinoflagellates simply do not spread.

Steamer clams (Mya arenaria) were associated with an otter midden on Sebree Point, July, 1972. Cleaned shells of butter clams (Mercenaria mercenaria) and cockles (Cardium corbis) occur along coasts where they might have been left by otters, but I have not found them with definite sign of predation. Shells of razor clams (Siliqua sp.) and horse clams (Saxidomus giganteus) are found very infrequently along otter-exploited coasts. These shells may have been left by otters. Some are found on altars, but even there, the shells could have been dropped by gulls. Otters have drowned in crab pots baited with clams (Scheffer 1953).

Although molluscs in the Glacier Bay area constitute a large biomass from which to draw, otters rely very little on bivalves as food. This probably reflects the fact that most of them must be dug from gravel, even at very shallow levels. Larger prey is available on cove bottoms with no need for digging.

3. Cephalopoda. Streveler saw a kit eating an octopus on the lagoon ice in Bartlett Cove in winter, 1971. Octopus (Octopus sp.) and squid (Loligo sp.) occur in moderate numbers in Glacier Bay and along the Pacific coast (Duggins and Quinn 1975, Quinn and Duggins 1977). The squid which wash ashore in Bartlett Cove are as much as 3.3 m long, more likely to eat otter than be eaten. Octopus were observed on the bottom of Goose Cove by

Dave Mills during dives in August, 1978.

Stephens (1957) found that octopus was a favourite otter food, but that no recognisable remains occurred in the scat. Predation on octopus might be fairly frequent in Glacier Bay.

E. Crustacea (Malacostraca)

1. Amphipods and isopods. Several species of gammarid and caprellid amphipods occur everywhere in intertidal and deeper waters in Glacier Bay, the Pacific coast (Quinn and Duggins 1977), and Muir Inlet. Small swarms move along the waterline during rising tides, and often cluster around fresh scats or feeding remains as soon as the tidewaters cover them (Home 1977). Some amphipods have been found in otter scats on the Pacific coast (Table 5).

Only one species of isopod has been identified in otter scat: Exosphaeroma, a shallow-water, intertidal animal often trapped in tide pools, as are amphipods (Quinn and Duggins 1977). Exosphaeroma has been found very rarely in otter scats on the Bartlett Cove dock, and at Reid Inlet (Streveler's logs).

In view of the small size of these crustaceans, and their low frequency in scats, it is evident that they are taken incidentally to the pursuit of other nektic crustaceans.

2. Shrimp. Pandalid shrimp are abundant everywhere in Glacier Bay. The pink shrimp, Pandalus borealis, composes 85% of the shrimp population not only in Glacier Bay, but in all of

southeastern Alaska (Ellson and Livingstone 1952, Ronholt 1963). Shoals of this shrimp provide the food base for an enormous biomass of predators - mysticetes, harbour seals, many species of sea birds, octopi, salmon, and halibut (Barr 1970, Butler 1970), and probably for harbour porpoises and other fishes, as well as otters. These shrimps occur as far north as the face of Margerie Glacier in Tarr Inlet. They probably occur at the faces of all other tidewater glaciers. But shrimps are more abundant in the waters of lower Glacier Bay than in the northern inlets. Quinn and Duggins (1977) found "a number" of Pandalus in the waters of the Pacific coast. Since feeding seals and whales are less numerous along that coast than in the waters of lower Glacier Bay, the concentration of shrimps is probably somewhat lower there.

The pink shrimp is eurybathic. Swarms are most abundant between 28 and 425 m (Ellson and Livingstone 1952, Ronholt 1963), but numbers occur in shallow waters such as those of Goose Cove, only 9 m deep. Many shrimp in Goose Cove and nearby waters are only 2 to 3 m below the surface.

NPS ranger Dave Mills sampled the pink shrimp population in Goose Cove in 1977 and 1978 with shrimp pots. Other species occur in the waters of lower Glacier Bay; but to date only P. borealis has appeared in Muir Inlet. It is less common there than in the more southern waters of the bay. Our hydrophone auditions in summer, 1978, found shrimp poppings about equal in incidence at all levels inside Goose Cove, in the open waters of Muir and Adams Inlet, and to within 200 m of the faces of tidewater glaciers.

But the frequency of poppings was much higher in Bartlett Cove.

In 1950, the second most abundant pandalid was the sidestripe shrimp, Pandalopsis dispar. This is the second most abundant species through southeastern Alaska (Ellson and Livingstone 1952, Ronholt 1963). In 1966, a species frequency of shrimps was reported for Glacier Bay which differed sharply from earlier studies. Yesaki and Kessler (1967) found the coonstripe shrimp, Pandalus hypsinotus, to be most common. This species was commonly taken in individual shrimp pots at Bartlett Cove in the late 1960's and early 1970's. Yesaki and Kessler found the spot shrimp, Pandalus platyceros, the second most abundant. P. borealis was not recorded at all.

Although no faunal incidence can be extrapolated beyond the period and circumstances of its study in Glacier Bay, this faunal change does seem a little extreme. At any rate, by 1975 the original species composition of shrimps resembled that of 1951 to 1956, when the studies of Ellson and Livingstone (1952) and Ronholt (1963) were carried out.

Pandalus borealis is the only pandalid which has spines on its abdomen (Ellson and Livingstone 1952), and can be identified easily in otter scats. The problem is that some well-chewed carapaces might belong to other species, and pass unrecognised.

The pink shrimp lives 5 or 6 years, and changes

sex from larval males to adult females at 4 years age. At maturity, most shrimps reach 13 cm in length (Barr 1970).

Predators on these shrimp in February and March obtain the added biomass of egg masses, which occur in 40% of the individuals taken. The next breeding season occurs in October and November (Feder and Paul 1977). Shrimp are most heavily preyed upon by whales and seals in Glacier Bay during summer. In winter, when egg-augmented shrimp are not available, the only predators likely to impact them are otters, some octopi, and fishes. But there is little evidence of winter shrimp-feeding by any of the pods of lower Glacier Bay or the Pacific coast (no winter data for Muir Inlet).

In winter in Thistle Cove, both otters and harbour seals occasionally evidenced shrimp-eating behaviour (III.2, below).

3. Crabs. Three species of crabs are eaten by the different Glacier Bay pods.

The Dungeness crab, Cancer magister, constitutes the largest portion of crabs (and of the entire food base) taken on the Pacific coast and in Bartlett Cove year-round. Individual crabs are common in waters as shallow as 6 m during the winter. There is no seasonal fluctuation in the occurrence of Dungeness crabs in the otter diets of most pods. Predation on crabs by mink, loons, goldeneyes, and ravens, seems also continuous and consistent throughout the year.

Rafts numbering seven or eight hundred Dungeness crabs with carapace diameters $\bar{x}$ = 5 cm wash up on the beaches of Dixon Harbour, and smaller numbers in Boussole and Astrolabe Bays in late autumn and early winter each year. The majority of Dungeness crabs found here and in other deposits average in size between 4 and 7 cm carapace diameter. Loons and goldeneyes bring up these small crabs in Thistle Cove during the winter.

Streveler (1977) believed that crabs of 7 cm and smaller carapace diameters were taken by preying mink. I have also seen loons struggling with crabs of this size, evidently with success.

In summer, most of the crabs taken by otters had carapace widths of 15 cm to 20 cm (this is also the legal minimum for human take) (Streveler 1975, 1977). Streveler concluded that the shells of smaller crabs were chiefly mink prey. In winter, however, I found smaller shells at otter feeding sites.

There may be no strict size limit among the crabs otters select at any time of year. Mink do not eat crabs at waterline as a rule, but carry their prey into the bush and often to the mouths of their dens. Any crabs found along shoreline are probably otter take, except when the otters are absent.

Of all crabs larger than 7 cm carapace diameter found in Thistle Cove feeding sites, otters account for at least 80%, and probably more.

Dungeness crabs are considered of only "moderate abundance" in the Pacific coastal waters (Duggins and Quinn 1975). Otters must be taking crabs from the minority of those of large size, selectively.

Dungeness crabs comprise the majority of winter prey taken by the Thistle and Barco pods (the two "roensis" strategies). The crabs are rare in Muir Inlet. Evidently this is a species which arrives relatively late in the faunal succession, and is not widely distributed in ice-choked waters.

The crab predominantly taken by Muir Inlet otters is the king crab, Paralithodes camschatica. This species also occurs in Bartlett Cove and along the Pacific coast, but at much greater depths, and is rarely taken by otters there. In June and July, soft-shelled king crabs occur in Goose Cove and Sebree Cove at depths 7 to 9 m and greater. No king crabs are taken from such shallow water in the lower bay.

Large smothers of individual king crabs move into shallow waters as moult begins, and are found at the heads of bays and inlets almost solely in that condition. In Icy Strait, the moult occurs in July and August (Harrison et al. 1942). Crabs are taken by Muir Inlet otters in late June and through the month of July. All carapaces and leg shells left from catches were very leathery, until early August. Crabs sampled from the bottom of Goose Cove in early August by our own collections were still soft-shelled, but the numbers of individuals in the shallows was

much reduced after mid-summer.

The Goose pod brought no more crabs in after the first week in August. Otter predation on king crabs is probably less a function of the crab's soft-shelled condition than to the fact that the crabs are only in this condition when in depths accessible to the otters. Shell hardness does not effect rates of predation on Dungeness crabs by otters.

King crabs migrate back into deeper waters at the end of the moulting season. These crabs are found at the greatest depths in Glacier Bay in mid-winter. The shells are hardest then, and the quality of meat considered at its highest for commercial purposes, but fishing is poorest because of the widespread dispersal of swarms (Harrison et al. 1942).

The average of carapace diameters for all the king crabs recovered from 7 m of water, low tide, in Goose Cove, was 15 cm. The same average size was evidenced by portions of carapaces left at feeding sites during June and July.

Another species of king crab, Paralithodes platypus, smaller than camschatica, is much rarer in the Icy Strait region (Harrison et al. 1942). This species has a distinctly bright-coloured carapace, and would have been identifiable had it occurred in any otter feeding remains, except scat. Any individuals of this species which moved into depths accessible to otters would be taken.

The low occurrence of king crabs in such shallow waters as those of Goose Cove suggests that only isolated individuals

wander into such insular waters. Otters probably hunt large individuals of this species as selectively as they do Dungeness crabs.

Tanner crabs (Chionoecetes bairdi) provide the poorest meat supply of any local decapods. (I have not found the abundant, but much smaller spider crabs - Pugettia sp., Hemigrapsis, etc. - in any otter scats or feeding sites.) Though tanner crabs are common in all the waters studied (Duggins and Quinn 1975), individuals of this species are least abundant in otter feeding sites. In summer dives, 1978, Dave Mills found tanner crabs in moderate numbers on the bottom of Goose Cove. None were observed in otter feeding remains.

Tanner crabs were infrequent in feeding sites at the north end of Wachusett Inlet entry, where king crabs were common. Two tanner crab carapaces, as fresh as the seven associated king crab carapaces, were left at Adams Inlet entry in late August, 1978.

Streveler records tanner crabs being taken and eaten on occasion at the dock in Bartlett Cove. In February, 1972, otters were feeding heavily on tanner crabs along the coast, from Bartlett Cove to Hutchins Bay (Fig. 5). This was one month prior to the onset of the crabs' breeding season, at least as recorded in Prince William Sound (Feder and Paul 1977). Ovulation may have begun slightly earlier in Glacier Bay; these crabs may have been heavy with eggs.

Tanner crabs were found infrequently in summer feeding sites on the Pacific coast (Table 5).

Unless augmented by egg masses, tanner crabs are clearly the otters' last choice among available crustaceans.

F. Echinodermata

1. Echinoidea. The extent and accessibility of sea urchin beds are directly proportional to the abundance of two other maritime mustelids, the sea otter and the mink. Echinoids constitute the chief prey of sea otters both at Amchitka (Kenyon 1969) and California (Shimek and Monk 1977). The seashore incidence of mink in parts of southeastern Alaska is proportional to the abundance of subtidal urchin beds (Harbo 1958, Croxton 1960).

Populations of sea urchins near the shores of Torch Bay and Dixon Harbour are of "moderate abundance" (Duggins and Quinn 1975). No urchins appear in otter or mink feeding sites there, winter or summer. (This coast is not optimal mink habitat ((Home 1977))).

Kushta otters generally show no preference for this item, but in some restricted areas, predation on urchins is quite high. I found many tests of Strongylocentrotus droebachiensis in an otter midden on Seabree Point in June, 1972, with Dungeness crabs and clam shells. Until 1978, I had never seen urchins in Muir Inlet. In that summer, for the first time, I found tests of the same species, measuring from 7.5 cm to 9.4 cm in diameter, on the island in Adams Inlet, at widely-scattered beach sites in the Goose pod's range, and on Sealer's Island.

Goose Cove NPS rangers Dave Mills and Rick Caulfield confirmed that no urchins had been found at those sites in previous years (though Adams Inlet is not so closely monitored as is Muir Inlet).

Very small numbers of urchins were being taken over a wide area of Muir Inlet, in the northernmost otter range.

On the shores of an extensive salt chuck system in the centre of Brownson Island, south of Wrangell, I found many mink and otter feeding sites littered with the tests of Strongylocentrotus droebachiensis, and probably other species. Otters were taking more of these urchins than were mink, despite the fact that fish and crabs were both abundant in the salt chuck. All otter middens on the rocky shores and promontories of this system were littered with urchin tests, from those freshly caught to shattered, weather remains dating from early in the summer. The one otter I observed feeding here was eating an urchin.

Clearly, predation on urchins was dominant and continuous throughout the summer in this area, despite the presence of other foods.

Several species of sea urchins occur in Bartlett Cove lagoon, over large areas of the lagoon bottom, but there are few records of otters preying on them. Since urchin consumption is rare elsewhere in Glacier Bay it also seems unlikely it will become common in the Muir Inlet pods. Probably the urchins taken in 1978 were among the first urchins encountered by these otters, and represent an exercise in experimental predation. The low return of biomass per unit capture effort probably determines low rates of predation whatever the frequency of the urchins.

Urchins seem as prey to be associated with poor swimmers, such as mink, or with thigmotter strategies, such as sea otters, but only exploited facultatively by trichotters.

G. Vertebrata

1. Chondrichthyes. Streveler had one record of the skate, Raja binoculata, brought to the Bartlett Cove dock by otters in September, 1968. The species is not known to be common.

2. Osteichthyes. Ryder (1954, 1955) and Erlinge (1969) have observed that otters catch mostly slower-moving fish. Salmonids are taken only when slower-moving species are not available. But there are long periods of time when the majority of the fish remains found in any otter feeding sites or scats in any of the Glacier Bay pods consists of salmonids. This is not true during spawning runs only, but may be found at any time of year.

Dolly Varden (Salvelinus malma) are taken actively from salt waters throughout the summer, and on many occasions in winter. When salmon run up freshwater rivers and into lakes in September, the otter catch amounts more to scavenging than fishing. The fish are often degenerating physically, and moribund, when taken from the water. Dolly Varden are, consequently, the fish most frequently taken by active pursuit in this area.

Only during spawning runs does the incidence of fish predominate over that of other foods in otter diets, in Glacier Bay.

Red salmon (Oncorhynchus nerka) migrating up the Yay River into Lake Andromeda were almost the only food exploited by the Boussole pod in September, 1974 (Streveler 1977).

In Anita Bay, Etolin Island, otters fed intensively on humpback salmon (O. gorbuscha) during the run of late summer, 1977. Water levels were so low the fish were often packed bank to bank in the diminished streams.

Chum salmon (O. keta) were taken in the lower Taiya River, west of Skagway, in a heavy run of August-September, 1974.

Remains of Dolly Varden are regularly observed in feeding sites on the Pacific coast, and in Muir Inlet, at rates of about one fish every three to four days. The same species is common in Bartlett Cove, but it is not the most frequently taken fish. The threespine stickleback predominates in otter scats on Bartlett Cove dock.

The skulls of Dolly Varden recovered from otter feeding sites in Thistle Cove averaged 7.5 cm in length. This indicates fish of 39.0 cm standard length, weighing 710 to 720 g (Dr. David Checkley, Department of Biological Sciences, University of Alaska, supplied the formulae and performed the calculations to determine these values). The largest individual skull was found at the mouth of Adams Inlet in August, 1978. This was 11.3 cm long, indicating a standard length of 58.8 cm, and weight of 2.46 kg. All Dolly Varden I have seen otters carrying orally out of the water

were between this record and the mean size.

In Muir Inlet, Dolly Varden are the most abundant salmonids. These fish comprise about 80% of the rather small proportion of bony fish in otter scats and feeding remains (Table 5). On the Pacific coast, fewer Dolly Varden are taken in winter than in summer.

Cottids - especially bullheads (Scorpaenichthys marmoratus) and Irish lords (Hemilepidotus hemilepidotus) - are common fish in lower Glacier Bay. On the basis of otter feeding remains, the fish are probably not rare in Muir Inlet. Cottid species constitute less than 20% of the fish catch in Muir Inlet. The same family may provide the majority of those unidentifiable bones which occur at about the same frequency (20%) in the scats from the Pacific coast.

On the Pacific coast, Cottus aleuticus and Leptocottus armatus occur in brackish and freshwater sloughs fished continuously by otters. These species probably account for unidentified fish bones in the Thistle pod scats; skulls of sculpins occurred at feeding sites there in winter. There is less evidence for sculpin catch in Bartlett Cove. Sculpins predominate in the fish catch of kushta otters near Sitka (Scheffer 1953), and are common otter catches on Vargas and Vancouver Island (Hatler, pers. comm.).

As swimmers, sculpins are inferior to salmonids in speed. The low incidence of such fish in otter diets may be a

reflection of the predators' disinclination to manipulate fish with such prominent pectoral and dorsal spines, and the greater quantity of internal bones, proportional to the volume of muscle, relative to that of salmonids. The lack of reflective surfaces may enable more sculpins to escape the otters' attention (III.3, below).

Threespine sticklebacks are the commonest fish consumed by otters in Bartlett Cove. They occur in many inland ponds in forested and alder-scrub areas, such as the escarpment pond above Boussole Valley, ponds in the saddle between Goose and Nunatak Coves, and landlocked ponds southeast of Goose Cove, in substantial numbers. Otters penetrate to and fish these ponds regularly or occasionally, depending upon the other resources of the season.

Gunnels (pholid sp.), capelins (Mallotus villosus), and herring (Clupea harengus) occur in all waters of Glacier Bay, Icy Strait, and the Pacific coast. In some years, large masses of herrings wash ashore late in autumn on the beaches of Bartlett Cove and Gustavus. I have observed mink swim from shore to catch live capelins and herrings in Thistle Cove during the winter. Such mink catches were never more than 6 cm long. Since mink have trouble catching any fish at all (Erlinge 1969), these species must be easily accessible to otters.

Hatler (pers. comm.) observed gunnels and minnows eaten by otters diving near the coasts of Vancouver Island. The

otters brought up fish in their mouths, and chewed them in the water. This is the only instance in which fish were eaten without being brought ashore (III.3, below). The posture of eating was indistinguishable from that of shrimp-eating, except for the absence of loud crackling noises. Such fish as these would be unidentifiable in scat, if they were well chewed before ingestion.

Eulachon (Thaleichthys pacificus) run up the Dixon River in late March. Remains of such oilfish would probably not be identifiable in otter scat, although the otters were fishing the river at the time.

The flounder, Platichthys stellatus, which occurs in salt, brackish, and fresh water on the Pacific coast (Murrell 1975) is probably eaten there, as it is taken by otters on Vancouver Island (Hatler, pers. comm.).

I have observed only one halibut (Hippoglossus stenolepis) catch by an otter. In late September, 1974, I saw a male otter climb aboard an anchored 6.5-m-boat in the cove south of Indian Point, near Juneau. The otter carried a 0.6-m halibut by grasping it orally by the spine, just behind the head. This otter dragged the fish up to the top canvas cover of the boat and retained the prey with its claws while it ate.

Cod were abundant in Torch Bay and Dixon Harbour waters in March and April, 1975. Cod skulls were found along the beaches, and were scavenged by other predators. None appeared with otter sign, though some could have been otter catches: cod are taken

by kushta otters in Britain (Harrison Matthews 1952).

3. Amphibia. Larvae of boreal toad, Bufo boreas, are abundant in all the freshwater ponds in which sticklebacks occur, and where otters are known to fish. I have no evidence of otter feeding on them, but tadpoles greatly outnumber the sticklebacks and, in August, are almost the same size. Both adult and larval frogs are common foods of inland otters (Liers 1951, Greer 1955, Stephens 1957, Field 1970).

I have on rare occasions found the carcasses of adult boreal toads on the banks of the Taiya River, near Skagway. The skin and flesh had been eaten entirely, and the bones and viscera had been left. This feeding pattern is characteristic of mink, but otters may occasionally take toads as they do in the interior.

4. Birds. Otters are repeatedly accused of making serious depredations among the chicks of sea birds, especially of glaucous-winged gulls, in nesting colonies in British Columbia and Washington (Kennedy 1968, Hayward et al. 1975, Foottit and Butler 1977, Verbeek and Morgan 1978), and in Prince William Sound (D. Calkins, pers. comm.; B. Kessel, pers. comm.; P. Mickelson, pers. comm.). Hatler (pers. comm.) reports several instances in which otters were active on nesting islands without taking any birds, and concluded that birds constitute only a small part of otter diets.

Otters were active on Sealer's Island during the

height of the nesting season in 1978, without leaving any evidence of predation on chicks or birds, despite the fact that otter sign demonstrated their activity over the entire surface of the island. During this season, both otters and birds (gulls and terns) share a common enemy: eagles. Possibly the otters take advantage of the protective cover afforded by those birds which immediately take to the air and hover, screaming, to protect the nests, in return for avoiding damage to the chicks, and are thereby given a comfortable and extensive feeding area for their marine prey.

This same pod, in the summer, 1977, allowed a pair of Canada geese to bring a brood of seven to fledging on the same ledge on which the otters rested habitually, as they did in the summer of 1978 (NPS ranger Rick Caulfield, pers. comm.).

Bones, feathers, and other remains of glaucous-winged gulls occur at low frequencies in the feeding sites of all the pods studied. Almost all individuals I discovered were of grey-plumed, immature individuals. Birds with this plumage are less than three years old (Gabrielson and Lincoln 1959). Remains of adults are almost unknown.

Verbeek and Morgan (1978) found remains of gull chicks in 82% of the otter scats left on Mandarte Island, B.C., by a single otter, between 7 July and 7 August, 1977. One otter alone removed 5.9% of the total fledgling crop in that year ("total fledgling crop" was defined by these authors as including those individuals whose survival would be predicted regardless of otter predation.)

These authors observed the same otter return to incompletely eaten birds on the night following the kills and finish eating them. This is exceptional behaviour for an otter (Solf 1972).

Otters kill birds by biting the backs of the birds' necks (Verbeek and Morgan 1978), and usually dismember the rest of the body. Wing and scapula are almost always removed. Carcasses found in feeding sites with skull and spine intact and without dismemberment, are then probably scavenged, not killed.

Most of the birds which washed in dead on the shores of Thistle Cove, and those left on Boussole beach by the 11 November storm in 1974 (glaucous-winged gulls, common murres, murrelet sp., etc.) were scavenged by the otters. Such carcasses lay on the beach for many hours before otters discovered them. Mink and weasels sometimes scavenged the birds before otters found them.

All these carcasses were eaten entirely, but none were dismembered, except incidentally to consumption.

Otters are said to cue visually on the white undersides of sea birds, and seize such birds from under water (Rodd 1873). Many of the hundreds of sea birds which coexist daily with otters in Thistle Cove all winter have white undersides - loons, common murres, and Barrow's goldeneyes. None of these birds display any aversion activity when otters are swimming near them.

Red-breasted mergansers were often killed at Bartlett Cove during the midsummer moulting season by otters who left the birds' heads on the dock. A male mallard was taken in Bartlett

Cove in 1969 (NPS files. unsigned). Buffleheads and goldeneyes found on the Bartlett Cove dock were dismembered in the manner of otter kills (Streveler's logs). All these birds are white-bellied.

I saw the Rowlee pod male carrying ashore a freshly killed pigeon guillemot in Wachusett Inlet, 23 August 1978. A male white-winged scoter was killed at Teacup Harbour on 27 June 1971 (Ole Wik's logs). These birds are dark-bellied; but were not necessarily killed in the water. The Rowlee male was carrying the bird 16 m from the shore, and moving parallel to it, when first sighted. I have encountered mallards along the shores of Thistle Cove in midwinter which could not be displaced into the water by anything but a close approach on foot. Such birds may be suffering from a thermal or nutritional deficiency, and would be easy prey for shore otters.

White bellies do predominate among kills, but are not the exclusive choice.

In Thistle Cove, scavenged birds are found more frequently on altars in winter than in summer. This is probably a reflection of the low food biomass available during winter, but the mortality of individual birds is also likely to be lower in summer.

Birds are incidental foods in the diets of otters, and scavenged birds constitute the majority of those eaten.

5. Mammals. Both voles and shrews may be the objects of systematic overland hunting of qamaniqs by winter otters, since

both are taken elsewhere.

Sign of small mammals is always highest in the qamaniqs around tree boles in winter. Shrew remains were found in otter scat in Thistle Cove, summer, 1975 (Table 5). Shrews are more likely to run out on the snow in winter than voles (Pruitt 1972). Otters do prey on shrews elsewhere, if never in large numbers (Greer 1955, Novikov 1956, Stephens 1957, Hamilton 1961, etc.). The identity of the shrew species is rarely given, as it is usually indeterminable in scat remains.

There may be a relationship between the fact that the northern water shrew, Sorex palustris, is the rarest of mammal species in Glacier Bay and southeastern Alaska. At an elevation of 360 m in the Sheep Camp valley of the Taiya River, near Skagway, water shrews occur and are seen fairly regularly, either in clear, quiet forest streams, or in the rapid, silty river (Home, in press). I have evidence of water shrews in the Yay River both winter and summer (Home 1977, in press). These shrews are present in only the most attenuated populations at low elevations.

There are no otters in the Sheep Camp valley, because the valley is cut off from the lower river by a steep-walled canyon of rapids and waterfalls. Below this canyon, otters do occur, and records for water shrews decline (although a systematic search has not been made here). Is the presence of otters a factor influencing the low levels of water shrew populations at low elevations?

Small rodents, perhaps taken incidentally in hunts for other prey, appear occasionally in the scats of most inland otters (Table 8). The systematic hunting of qamaniqs in Boussole Valley and around Thistle Cove indicates that small rodents are sought actively. Evidence for success during winter is nonexistent. On the evidence, more energy is expended in hunting than would be returned by consumption of the rare catch.

But when populations of shrews and voles were at cyclic lows on the Pacific coast, the Thistle pod rarely hunted on shore, even though it was active in the cove every day.

Vole populations were at a high level in Muir Inlet in the summer, 1978. Voles were active everywhere around Goose Cove, in all vegetated areas, and as far inland as the Dryas mat extended. Dead voles lay unscavenged on the grass fringes of the beach daily. Other scavengers ate them while the otters were in view. A live vole kept open a burrow in the centre of the Goose pod's habitual feeding and resting ledge, unmolested, for weeks, after the otters first occupied this ledge in early August.

Larger mammals - minks, sumpfotters, hares, beavers - are taken by inland otters (Novikov 1956, Greer 1955, Field 1970). No beavers or hares are available in Glacier Bay.

Larger mammals have been scavenged (Harris 1968). A dead sea lion washed in on Astrolabe beach in mid-November, 1974, and was carried piece by piece behind the dunes by a bear. The largely cleaned carcass was subsequently scavenged by wolves. The adults of the Boussole pod made a rare visit to Astrolabe beach to

go directly to this carcass. I can not confirm, from subsequent scat evidence, that the otters fed on the meat (as I can for the wolves), but if any remained, I am certain that they did so.

Wolves have scavenged harbour seals found on this beach in summer (Streveler 1975). Otters might take advantage of such carcasses if found.

But Field (1970) was unable to induce some Michigan otters, one pod of which exploited a food base almost as marginal as that of Boussole Valley, to scavenge carcasses of white-tailed deer left for them.

H. Foods Available, and Disdained

1. Plants. Ryder (1954, 1955) found plant matter to be the largest volumetric component of the stomach contents of a series of otters sampled in Michigan. He considered the material ingested incidental to the consumption of animal prey. Clay and sand are frequent components of otter scats along the maritime coast, and even among inland animals (Liers 1951), for the same reason.

Stroganov (1962) described inland L. lutra eating grass, young tree shoots, and bark, not incidental to the taking of animal food. Insects or larvae may account for the otters' approach to these materials.

No plant matter has been found in the scats of any otters in southeastern Alaska.

2. Animals

Red, yellow, and green colonial tunicates, colonial hydrozoans, bryozoans, jellyfish, as well as spider crabs, have all been found in beach detritus along the beaches habitually exploited by otters. The polychaetes are similar to marine polychaetes eaten by sea otters (Kenyon 1969).

In the case of large wash-ups, such as those resulting from the 11 November 1974 storm, satiety may account for the otters leaving behind so much of the biomass. But many of these deepwater benthic forms must have been unfamiliar to the otters (only one such deposition was observed in two years).

Otters elsewhere eat starfish (Stephens 1957, Harris 1968), which are common everywhere in Glacier Bay, but have never been found associated with otter feeding.

I. Discussion

From the details of the previous accounts, and comparison of Tables 5 through 9, it is evident that there is a difference of degree of the exploitation of prey between the biochronologically oldest environments (the Pacific coast), the intermediate-aged (Bartlett Cove), and the recent (Goose Cove) environments. This variation in the prey pattern is related to the overall faunal composition, which varies from site to site, relative to the course of postglacial succession.

All these otters are principally crustacean feeders. These pods select larger crabs than the average in local populations. When there is no annual fluctuation in the incidence of a given crab species, such as the Dungeness crab, there is similarly little variation in the annual diet of the otter. Where there is considerable variation in such availability, as with the king crabs in Muir Inlet, the otters' diet shows a greater seasonal variation accordingly.

When king crabs are available in shallower waters, the otters take them in preference to shrimp. Once the crabs have moved into deeper waters, the otters take far more shrimp than previously, even though the incidence of shrimp does not change during this period. The choice species or individual is always that which yields the largest biomass per unit capture effort.

Fish, and probably birds, are taken incidentally to the pursuit of slower-moving crustaceans. Otter foraging strategies are structured preponderantly around the habits and movements of crabs and shrimp. Within these structures, any other edible species are taken as opportunity allows.

Salmonids may be taken secondarily to slower-moving fishes in inland waters (Ryder 1955), but in Glacier Bay, the faster-moving salmonids are often taken in greater numbers than slower-moving fish.

The pods of the Pacific coast and Bartlett Cove exhibit the greatest diversity in diet. The Goose pod has the least opportunity to diversify its diet. When new arrivals do appear in

the Goose Cove area, these animals are immediately sampled to determine whether they can be added to the diet.

The degree of prey choice, the frequency of activity in salt, relative to fresh, water, and of the overland activity relative to aquatic activity, are all initially structured by the features of the terrain accessible in the range of the pod.

The specific topographic character of the range and, where applicable, the degree of postglacial succession, determines the basic strategy. When a strategy is successful, as the "phocoid" strategy seems to be in Goose Cove, this strategy is retained, howevermuch the ecosystem around the otters changes. The otters' well-known conservatism of range exploitation will maintain the initial foraging strategy.

Postglacial changes increase the potential food resources and diversity in marine, as well as terrestrial, habitats. Confronted with a sea face of unstable and faunistically depauperate sand, the Boussole pod is forced to utilise as its focal water a slough system, even though this system is poor in food resources. The pod is accordingly influenced heavily toward overland hunting. No further succession is likely to change the faunal resources available; the Boussole pod is accordingly the most nearly marginal of all these pods, its continued existence at risk, should a year of low small mammal populations coincide with poor fish runs or declines in other species. Scavenging large mammal carcasses is an important strategy in the annual activities.

With the Thistle pod, the diversity of resources is sufficient that any single catastrophe, or even more than one, could be compensated for. When small mammals are abundant, they are hunted; when not, they are dispensed with. If the river's resources are destroyed by a jökulhlaup, harvesting of the higher forest floor can be attempted. If the cove itself becomes too silty to support any more life, the river valley and open harbour can be exploited more continuously. Such alternatives probably support otters through years of catastrophes - and catastrophes are a regular feature of life on this coast (Table 2).

The Goose pod has found its focal water a structure which concentrated the choicest food species to such a degree that it never became necessary for this pod to develop any exploitation of adjacent resources, beyond punctuational and experimental forays into the muskeg ponds. Despite the complete change in the ecological character of the cove since the pod took up residence there, there appears to have been minimal or no change in its strategies of foraging.

The Goose otters may be exhibiting some parallels with sea otters, which will eat bird flesh only if starving (and the flesh passes through their guts undigested); they will not eat mammal flesh, even if starving (Kenyon 1969).

III.2. HUNTING AND FISHING TECHNIQUES

A. Musselling

Carl (1966) reported that otters pry mussels off pilings in Victoria and Vancouver harbours, but did not describe the technique. The largest amounts of mussel shell occur in scats of the Adams Inlet pod; I know little of this pod's habits. Stephens (1957) observed otters biting off one end of a pair of mussel shells, although the kits could not open the shells by themselves.

Mussels grow in the deeper parts of the intertidal zone in Goose Cove, but not on the bottom. Each shell is positioned with its margin perpendicular to the substrate. The shells are tightly packed with no detectable interstices between their snouts. The sharp margins thus exposed constitute a carapace-like surface which must be difficult to penetrate. (Black bears smash mussels in beds by rubbing one forepaw brusquely over the bed, then licking the detritus and juices from their paws ((M. Nigro's log)). Such broken shells might be mistaken for otter prey.)

Tiny triangular shell fragments are frequent in otter scats in Muir Inlet, indicating that otters masticate parts of the shell, and that these parts pass through their intestines in this sharp-edged form, and in some quantity. I have not found

intact mussel shells which bore the marks of otter bites.

I made only two observations of an otter attempting mussel extraction. Both of these were in Goose Cove, at low tide, and both late in the evening, when visibility was poor.

From 2300 to 2330 on 19 August 1978, and from 2130 to 2150 on 21 August 1978, I saw the female, accompanied by her kits, active in a mussel bed on the east side of Goose Cove. Part of the bed was exposed, but most of it was still under ~18 cm of water.

The female stood over the bed in water up to her belly. Bracing her legs, she stuck her head completely under water for intervals of 10 to 12 sec. These semidives (IV.5, below) consisted of sessions of tugging and pulling with the mouth, moving the forepart of the body from side to side parallel with the clavicular axis, with much twisting of the neck and shoulders. I did not see any sudden retraction of the head to indicate that she had broken a mussel loose. Mussels still submerged were presumably easier of access than those exposed, since aerated mussels clamp their shells tightly shut.

B. Shrimping

I observed success of shrimp capture in 70% to 88% of dives, in dive series lasting 25 min, in Goose Cove (IV.5, below). Hatler (pers. comm.) recorded similar rates - 87% in one series near Vargas Island, B.C. Such rates may be typical for this

strategy. Other, larger prey are taken in such dive series, incidental to the pursuit of shrimp.

Shrimping dives only rarely occur during winter on the Pacific coast, and evidently are not common even in summer (Table 5). The Goose pod's August foraging was devoted entirely to shrimping. Shrimping is carried on to some extent even when king crabs are the chief object of predation.

Shrimping is distinct from all other otter feeding strategies in that the otter remains in the water to eat. Once a shrimp is taken in the mouth, the otter surfaces with its nose pointing upward, submerges the rest of its body, treading water, so as not to strain the muscles of the throat. The otter keeps its nose upward while masticating, so as not to spill the mouth contents. Three or four chews are usually sufficient. The otter swallows and dives immediately.

If there is a swell across the water surface while the otter is eating, the animal positions itself so that waves break across the back of its neck.

The same nose-up, crackling chewing is only rarely exhibited by otters in Thistle Cove in winter. Harbour seals there occasionally exhibit the same behaviour.

Similar diving and feeding behaviour has been observed on the coast of British Columbia by Hatler (pers. comm.) when otters were taking minnows and gunnels. Hatler observed only a 58% capture success in dives devoted to this fishing.

Hearing is the otters' most important sense (Savage 1957). The repeated snapping noises made underwater by shrimp may be the cue by which otters locate shrimps. The female and kits, when underwater together, make a continuous trilling (IV.3, below), which does not influence the incidence of shrimp noises. Since adult otters do not make these noises when diving alone or together, the sound is not integral to the shrimping strategy.

Dependence on shrimp seems to be the critical step in developing freedom from dependence on the land, and adapting to completely marine foraging. The semi-dives observed in musselling represent the most primitive stage in the exploitation of marine food resources. Fishing is an intermediate stage, in which the otter must move to the shore to eat, regardless where the fish is caught. Fish such as gunnels and minnows initiate a stage of foraging in which it is no longer necessary to return to shore, but the success rates in the catch of such small fish seem to be lower than success rates in shrimp catch, which may initially determine a lineage to concentrate on shrimp.

With shrimping, a foraging strategy which is completely self-sufficient in the water, and also has a high rate of biomass return per unit capture effort expended, is achieved. Hard aerial surfaces are thereafter required only for resting.

C. Crabbing

Otters generally carry crabs ashore in the otter's mouth, grasping the rear end of the crab's carapace. Crabs are

less often carried to feeding sites away from the water's edge than is any other prey taken from the water. Dungeness crab remains are often found at random feeding sites on the beach. (Fish, by contrast, are usually carried to altars or other preferred feeding sites.)

The difference may be a reflection of the difficulty in carrying crabs orally. Most fish are limp when carried ashore; most crabs are still squirming when brought out of the water.

This indisposition to carrying small crabs far from the sea is not invariable. When crabs are left near the waterline after eating this may be a function of the intensity of the predation at the time. Otters may eat one crab rapidly at the nearest shore point to the capture and then return to the sea for more. But the fact that most remains are solitary suggests that this is not the case, at least during winter.

The carapace and other shell pieces of Dungeness crabs are left behind. The viscera are usually eaten. The legs are sometimes bitten off just at the water's edge, and the cephalothorax carried farther inland. In most cases, the legs are eaten entirely, and no remains of leg shell are left.

Legs of king crabs are always carried to feeding sites well away from the water, as are fish. Otters do not eat the viscera of king crabs. Parts of the same crab may be distributed among several feeding sites, as if one crab were sufficient for the entire pod (III.4, below).

The deepest dives in evidence for any pod in Glacier Bay may be those made in pursuit of king crabs around Sealer's Island (IV.5, below). These deep dives are abandoned once the king crabs no longer appear in feeding sites, which must be a consequence of the crabs' moving out of shallow-water moulting grounds into deeper waters.

D. Urchining

All urchin tests found along the shores of Muir Inlet and on Sealer's Island, in summer, 1978, had been transported to feeding sites intact. Some of these sites were high on the island. The urchins had been carried orally up a slick algiferous cliff 4 to 5 m high, and on a linear walk of 35 to 40 m from the cliff's edge over tundra and krummholz.

After that, the tests were broken. All pieces of the test were at the same site. Most urchins were broken only at one end. Less than a third of the shell was broken and removed. Such breaks were irregular, but not shattered, and must have been made by a bite. There was no removal or breakage of the spines either on the remains of the test, or on the smaller fragments.

Some freshly taken tests in Brownson Island were broken in half; some were shattered.

E. Fishing

Ryder (1954, 1955) formulated three principles characteristic of otter fishing in Michigan. (1) Fish are preyed upon in inverse proportion to their swimming ability. Salmonids are taken only when slower-moving fishes are not available. (2) Given this fact, otters capture fish in proportion to their abundance in the waters only to a limited extent. (3) On any but the smallest streams, predation on fish seems to be insignificant as a factor affecting the population dynamics of most fish species, even when the otter population is at maximum density. Erlinge (1969) agreed that otters catch only slow-moving fish.

The preferential selection of salmonids shown by Glacier Bay otters may be related to fluctuations of species incidence in the waters, to concentration levels of individuals of single species, or to other factors in the cuing on, or the pursuit of, fish, by the otters.

The turbidity of water in Thistle Cove and other glacial-outwash bays would seem to render impossible any visual cuing on fish by otters. In rivers and lakes without glacial influx, such visual cuing may be effective. Zeller (1960) found that a captive saro (Pteronura) chose fish proportional to the degree of reflectivity of the species's scales in the water. The most brilliantly reflective fish were taken preferentially. Preference declined proportional to the reduction in reflectivity of the scales. In the rivers and sloughs of their tropical forest homes,

saros occur only in quiet "blackwater" streams, where the water is turbid (Simon 1966).

In turbid waters, the high reflectivity of such fish as salmonids may be the factor influencing the otter's choice of them as prey. The less reflective fish may not even be seen. The occasional glitter of a silver-sided salmonid in otherwise murky waters may be the factor which alerts a diving otter to the fish's presence, and may be the reason that most of the fish taken by Glacier Bay otters are salmonids (80%).

In terms of biomass yield per unit capture effort, salmonids surpass the yield of other fish species. Experience that such reflective glints perceived in the water yield the greatest amount of meat may reinforce the otters' reliance on visual cuing.

Given the turbidity of the water, the frequency of visual perception of the occasional flickers (except during spawning runs) depends on the proximity of the otter to the fish at the moment of illumination, and the angular position of each relative to the other. This may be the factor decisive to salmonid catch.

Like Lutra, the saro is a trichotter. Visual cuing must then have some importance for trichotters. Thigmotters, such as sea otters, despite having vision competent for discriminating specific sizes and shapes (Gentry and Peterson 1967), do not cue visually underwater (Shimek 1977, Shimek and Monk 1977).

Most other fish taken by Glacier Bay otters are dull-coloured and slow moving. Since fish are seized orally behind

the skull, or at the midpoint of the fish's spine, otters must seize such fish from above, grasping the darkest part of the fish's body.

I have never seen otters surface with fish which were damaged, scratched, or bleeding from any other sites than that grasped by the otter's mouth. Evidently the fish were initially seized in this position, and are not transferred in position after being caught.

The halibut I observed one otter drag up the side of a boat in Indian Point probably weighed between 4 and 5 kg. The otter carrying this fish was the largest individual I have seen in southeastern Alaska. Hatler (pers. comm.) observed an otter drag a 1.67-m wolf eel (Anarrichthys ocellatus) onto the shore of Vancouver Island. A trained Indian otter weighing 8.2 kg was able to capture and land an English pike weighing 9.4 kg (Gudger 1927). A wild otter can thus capture fish which outweigh the otter.

During salmon runs, otters may carry fish from the streams only as far as the nearest rock, and take only a few mouthfuls from the mid-body of the fish, where the muscle reaches its maximum swell from the sagittal line. Fish found at streamside, with only part of the flesh consumed, are more likely to be otter catches than those of any other predator.

F. Ornithivory

Bird kills, as distinguished from scavenges, are infrequent anywhere in southeastern Alaska. There has been little

evidence of otter predation on chicks in nesting colonies, although otters have been present on islands where nesting colonies exist.

Evidently in the water there is some take of birds which have white undersides (Rodd 1873). The exact mode of killing has not been described.

Bird capture requires that the prey be carried ashore to be dismembered and eaten. A rock or ice surface must be utilised. The complex, much-jointed avian body must be taken apart in stages, with varying degrees of pressure applied in movements requiring more force than that needed to dismember a decapod or fish. The amount of energy expended in obtaining and consuming a unit of avian flesh must be greater than that expended to obtain an equal biomass of crabs or fish.

Evidently otters bite off the heads of birds taken alive, but I have seen individuals carrying birds with the heads attached; perhaps only the neck is broken until feeding begins. Heads of mergansers were often left on the dock at Bartlett Cove.

This strategy is a limiting factor in otter adaptation to wholly aquatic exploitation.

G. Mammal-hunting

Small mammal remains have been found in otter scat only in summer (Table 5). Hunting of mammals in winter is evidenced at considerable intensity in the Boussole Valley, but

seems incidental in other pods.

In the interior of Alaska, qamaniqs are vacuums in the subnivean realm of small mammal habitats. The subnivean temperature on the forest floor beneath qamaniqs, where the snow is thinnest, is much lower than that under the thicker api around the qamaniq (Pruitt 1972).

In southeastern Alaska, subnivean temperatures rarely differ from ambient air temperatures by more than a few degrees. Mammals active under qamaniqs in southeastern Alaska are not reacting to thermal stress equal to that of mammals in the interior. This is evidenced by the fact that small mammals track continually in and around the surface of such qamaniqs in southeastern Alaska (Home 1977).

There is more sign of small mammals within qamaniqs than elsewhere on the forest floor api in southeastern Alaska. Otters hunt the qamaniqs systematically in winter, as do most other carnivores. This hunting may be performed by the solitary male, except in the Boussole pod. Unlike the other predators which also hunt these features, otters never dig into snow burrows. Evidence of mammal capture was never found.

The Boussole male's overland hunting was carried out even during a winter of low abundance of small mammals. Overland tracking may not be correlated inevitably with foraging.

H. Scavenging

The scavenging of birds, invertebrates, marine mammals, and occasional fish, along the Pacific coast, is an important source of otter food through winter and summer. It may be critical during winters. Any strand line or wash-up left by storms, or by seasonal die-offs, is searched systematically by the entire pod.

The size of items scavenged from beaches by otters ranges from that of herring-sized fish to carcasses of sea lions. Much of the fish biomass obtained during spawning runs, especially when death rates among the fish begin to climb, can be considered scavenge rather than kill.

Since birds and other carcasses often lie along the beaches for hours, or may be scavenged by other predators, before the otters locate them, it appears that there is no systematic activity directed toward hunting carcasses on beaches, except in the aftermath of large storms and other exceptional injections of biomass.

The Goose pod evidently does not scavenge the shore. No food item recovered there indicated scavenging of marine resources.

III.3. EATING ACTIVITY SITES AND SCATOLOGY

A. Incidental, or Random, Feeding Sites

Remains of otter feeding are found at random points along rocky shorelines and gravel beaches of any focal water used by the pod, and along remoter parts of the shore. The solitary male uses no regular feeding sites when away from the focal water.

Feeding remains at the entries to dens (e.g., the birds left at the cliff top den south of Thistle Cove) are so infrequent as to come under this heading.

In-water feeding, which occurs only during the foraging for shrimp, represents a special case which could be classified as random-site feeding, since the otters do not surface in any particular sector of the focal water.

There are no features common among random sites, except the fact that sand and mud surfaces are almost never used. (Sand surfaces may be the site of eating activity if detritus is being scavenged; mud, never.)

Shore points nearest to the surfacing otter are usually the sites chosen for random eating, regardless of other factors. Crab shells were often left only 3 m from my front door in Thistle Cove.

No effort is made to convey food above the high tide line at random sites. Incidental feeding remains are removed at each high tide.

Isolated feeding remains not only away from the focal water, but even those left in unusual places around the focal water tend to be remains of the solitary male's feeding. The female and kits use habitual sites or middens much more than they tend to leave food at random sites.

Feeding sign at Bartlett Cove is rarely left at random points, but there is another factor (below).

Random feeding sign was found less frequently in winter on the Pacific coast ranges, than in summer. This may indicate that the winter food supply is less than that of summer.

B. Middens

Piles of detritus, both of feeding remains (crab and mollusc shells, bones, etc.) and of scat, left at habitual feeding sites along shores not otherwise distinguished by a specific rock formation constitute middens. Such accumulations may occur on rock surfaces or on gravel beaches. Identical accumulations on elevated rocks are styled altars (below).

These accumulations rarely build up along beaches, because storms and other weather effects tend to disperse loose piles of shell and test fragments. Such piles survive longer on elevated rocks. Otters respond negatively to the removal of their scats and feeding traces (below), and tend to abandon use of such sites. The tendency to concentrate middens on high rocks (altars) suggests that otters conserve such deposits as territorial markers.

Middens may survive on formations of lower elevation wherever there is protection from high waves and heavy rain run-off, above maximum tide line. I found one on shore rocks on the west side of Sebree Point, summer, 1972, which seemed to represent a whole summer's feeding by one pod. It contained crab shells, clam shells, and urchin tests, broken, and all contents deeply layered.

I found large piles of crab shells, and especially of urchin tests, around the rock shore of the salt chuck system in Brownson Island. None of these sites were elevated above the surrounding shore; there were no altars available. Headlands were the preferred sites, in proportion to the distance of the point of the headland from shore, with maximum waterline around each headland.

Headlands projecting farthest into the water formed surrogate altars, and were the most heavily littered. None were isolated from shore at high tide.

C. Altars (Batten 1953)

Large, sarsen-like rocks near the focal water are habitually chosen by otters as feeding sites. Elmhirst (1938) believed such sites were preferred by the otters because the summits afforded views in all directions. The animals could remain on watch while they ate.

Similar feeding sites in Alaska, however, occur on ledges along cliffs, sometimes concealed by vegetation, from

which visibility is extremely limited. Some altars have trees growing from their summits, with underbrush, which impede visibility of half the panorama from the top of the altar.

Isolation, not elevation, determines preferred feeding sites. Anchored boats, docks, and rocks entirely surrounded by water (at least at high tide) are all chosen in preference to a lofty rock some distance from water line.

But along the tide line of any focal water, such high rocks can be predicted as preferential feeding and scat sites, whether or not they afford panoramic views. Rocks otherwise identical in shape are unlikely to be used, even if they command more open vistas, when they stand more than 10 m from the tide line.

The Goose pod's habitual feeding ledge can be classified as an altar, because it is elevated, and is reached by a climb up steep rock cliffs. Today, this ledge is concealed by vegetation, but this was not the case prior to 1965 when the pod first occupied the cove. Growth of the vegetational obstruction has not affected the pattern of use.

Some altars around the focal water of a given pod may not be used for weeks at a time, but all altars tend to be used more or less equally in the course of a year's activities.

The two most prominent altars in Thistle Cove were fed on frequently during the two winters that I studied there, but scat was never left on them. This partial reduction in function was probably a response to my own activity, on a daily basis, near both

these rocks. Much more use of the altars was observed the following summer, when human intrusion on a daily basis was much reduced.

D. Expanded Surface Sites

At Rowlee Point and Point McLeod, in Muir Inlet, there are many elevated points along the staircase-structured rock of the shore. These rocks qualify as altars, even though some are only 1 m above the surrounding rock level. Scat and feeding sign are deposited not only on these altars, but distributed continuously over the surface rock from one altar to the next.

The zone so defined by the distribution of feeding remains and scat, including a number of rocks of varying elevation which function as altars, extended 130 m from one end to the other. All of Rowlee Point was included, and the zone stretched south from the point. Rock layers to the west of the point are similarly formed, but were not made use of.

There was a similar situation on the north shore of Adams Inlet entrance. Otter scats occurred at the summits of all altars along 0.75 km of coastline. The concentration of scats was heaviest on some isolated rocks at the mid-point of this segment of the coast. Surface deposits littered the ground between the altars. Single deposits of scat and feeding remains also occurred within the Elymus zone, despite its sandy surface; this is unusual. Feeding sign was also found on isolated ledges within the formation.

Such extensive deposits, which are unique to these two sites within Glacier Bay, should be designated "chancels." Chancels are defined here as areas of scat deposition and feeding activity which include (1) altars, and (2) all of the intermediate rock or gravel substrate around any one, or between two or more altars. The elevations of the rocks involved may vary by as much as 5 m from the lowest to the highest scat deposit (an observation which is not critical to the definition.)

Unlike middens, chancels extend to, and often below, high tide line. In July and August, most of the scats left below the tide line at Rowlee Point contained king crab remains. Scats composed principally of shrimp were not distributed with any correlation to tide level. Most scats above the highest tide line contained fish remains.

Since scats are deposited within an hour of the otter's feeding (Liers 1951), it is possible that these correlations reflect the relationship between prey pursuit and tide levels at the time of pursuit. Crabs might be pursued only at low tide levels in the waters adjacent to Rowlee Point. The bottom here slopes as steeply down to the 18.75 m contour as does that on the north and west side of Sealer's Island. At high tides, crabs are thus 6 to 8 m deeper than at low tide. Fishing efforts might then be concentrated at high tides simply because of the relative inaccessibility of the crabs then. Shrimp fishing is never related to tide levels.

No such relationship between scat remains and tide levels has been observed in any other pod.

In August, all fresh scats at Rowlee Point were deposited serially higher and higher above the level, not only of tides, but of previously deposited scats. This was the only degree of serial rotation observed in scat deposition.

The development of chancels from initial altar sites reflects a complete absence of disturbance to the otters using the sites. NPS ranger Cornelius' logs reveal that in 1969, the same Rowlee Point sites were used and in the same patterns as those I observed in 1978.

Chancels would develop and spread rapidly if the same pattern of scat deposition were retained throughout a season, and the scat was not eroded by weather effects.

Sealer's Island is unique as a feeding site formation among the otter pods of Glacier Bay. The entire surface of this rock dome is covered with an evenly-distributed set of feeding sites, each including scat deposits. These sites are not only located along the edge of the island, at the top of 3 m cliffs, but over inland slopes; one is located at the island's highest point.

Some of the sites are not single, but can be classified as middens. Most sites represent single feeding or scat deposits. Most of the remains are on the south and east side of the island, adjacent to the shallower waters between the island and the mainland.

Sites were less numerous on the north and west sides, adjacent to much deeper waters. All were composed of king crab remains, but included urchins, Dolly Vardens, and other foods.

Sealer's Island is, in effect, an altar with an extremely broad surface. There is no single rock on the surface to qualify as an altar. The steep, slick-sided cliffs which abut the island on all sides are characteristic of single altars. Otters appear to have a specific spatial concept of the altar, a landform of elevation and isolation, affording a variety of sites accessible to the waters in which the otters are foraging. It need not provide any protection from predators or competitors, since brown bears and other predators do reach the island during bird nesting seasons.

This is an altar gone to gigantism. I call such a rare formation a "shetiyyah."

E. Discussion

Most investigators (e.g. Novikov 1956, Erlinge 1968, 1969) have acknowledged that there is a rota of use frequency in feeding sites, even around focal waters. Serial use of each of the habitual sites in the course of a season has been observed in Goose Cove. In Thistle Cove, site rotation seems confined to the random deposition of feeding remains on the western side of the cove. There is less evidence for site rotation in Bartlett Cove. There are no regular feeding sites in the Boussole pod's range. This is also characteristic of inland river otters, at least in

winter, occupying marginal foraging range (Field 1970).

Use of altars and middens continues for years at a time. All those in Muir Inlet have at least a ten-year history. Elmhirst (1938) observed continuous use in Scotland for thirty years and more.

Otters are sensitive to human interference with their feeding and scat sites, even though most pods show no special response to human presence otherwise. Otters once ate their prey on the boat dock in Bartlett Cove, first built in 1958. A surface beam about 30 cm above the dock level divided the dock into two sections. The otters ate only on the lagoonward side, and left scat only on the shore side.

In 1977, the shoreward side of this dock was removed. After that time, the otters left no more scat anywhere on the dock.

This clear separation of feeding from scat areas is unique in the Glacier Bay area. It may reflect the special character of a man-made dock subsumed as an otter territorial marker, while human activity was a daily occurrence. Certainly the Barco pod regarded the elimination of its regular scat-deposition bank as a territorial affront, which has influenced its behaviour since that time. The pod eats less often on the dock than it did before.

When I removed all fresh scat from the Goose pod's resting ledge late in August, 1978, the pod abandoned use of this

ledge for eight days, although it had been active there without interruption for a month previously.

F. Scatology

Otters produce more substantial amounts of scat, daily, proportional to their body weight, than do most other mustelids (Erlinge 1968). Greer (1955) observed two inland otters deposit three separate scats in ten minutes. This must mean separate deposits. The amount produced in one defecation depends on the food material, and may vary from a single scat to a deposit of four or five.

After a half-hour shrimping session in Goose Cove, each adult left one large scat deposit. One of these contained four separate scats, and the other, five. The kits left single scat deposits, about half the size of one adult scat.

Otter scats are released from the rectum encased in a thick mucus, which protects the anus and gut lining from the sharp edges of shells and carapace fragments (Stephens 1957). Stephens found that the scats of young otters were often streaked with blood. I have never seen this. Some fresh scats, including adult scats, have the dark red-brown hue of dried blood, but the colour is not a surface deposit. It perfuses all the material in the scat. It may be colouring matter derived from prey. This colouring fades as soon as the mucus dries.

The majority of scats are dark grey in colour, when fresh, and become lighter grey as they dry.

Scats dry rapidly, and are readily disintegrated in tidewater or rain. After immersion, the contents of a scat slump into inchoate masses. Mussel shell fragments are the first to become detached, even from uncrumbled scats, once they are dry.

Attempts to collect fresh scats regularly are likely to result in displacement of the otters. For this reason, I was not able to collect fresh scats regularly from sites still being used actively by the otters. I did so on occasions preceding my absence from the pod's range.

Individual adult scats ranged from 2.5 cm to 8.9 cm in length, and from 1.6 cm to 2.4 cm in thickness. Those of the two kits in Goose Cove were from 1.5 to 3.8 cm long, and 0.9 to 1.7 cm in thickness. Table 13 lists the weights and measurements of several scats collected when only hours old, oven-dried in the lab without the addition of preservatives. These are typical in size of the crab-, shrimp-, and fish-containing scats seen in the Goose and Rowlee Point pods.

TABLE 13. SCATOLOGY

Weights and measurements of freshly collected scats, from Goose Cove, August, 1978, after oven-drying. No preservatives were added.

Origin and contents	Dimensions	Weights
1. Rowlee Point		
King crab		12.50 g
Crab, prob. all king		5.74 g
Fish bones, unid. (cottid?)		9.69 g
2. Sealer's Island		
Shrimp		8.25 g
Shrimp	5.45 x 1.8 cm	
	5.75 x 2.5 cm	7.33 g
	1.6 x 2.6 cm	(one deposit)
3. Goose Cove		
Shrimp	2 cm thick	9.42 g
Shrimp	8.9 x 2.5 cm	8.30 g
Shrimp	3.9 x 1.6 cm	7.93 g
Shrimp (kit scat)	3.9 x 1.0 cm	
	1.5 x 1.1 cm	3.80 g
	2.3 x 1.3 cm	(one deposit)
Shrimp (kit scat)	3.8 x 0.9 cm	5.1 g
	3.4 x 1.7 cm	(one deposit)

$\bar{x}$ of scat weight = 8.66 g

($\bar{x}$ of scat weight of inland otters = 7.6 g (Field 1970))

III.4. NUTRITIONAL OBSERVATIONS

A. General

Captive adults of Lutra lutra eat about 1 kg of animal protein per day (Novikov 1956). Harris (1968) fed adult L. canadensis under experimental restrictions, and found that these otters ate 1.36 kg of food per day, and never more than 0.45 kg at a single meal. The food he offered these American otters included commercial preparations, designed for mink farms, of ground offal meats and supplemental nutrients. Fish, prawns, mussels, and other natural foods were added.

Mink eat 20% of their body weight each day if the food is composed entirely of mammal meat, but more, if the food is fish (Novikov 1956). Harris did not specify whether his otters' food intake varied relative to the identity of its contents.

Harris's specimens were probably inland otters collected in the eastern part of North America. Such otters are, on the average, the smallest of any L. canadensis (Jong 1972). Even near the west coast, maritime otters are larger than inland otters (Cowan and Guiguet 1973). The precise degree, and the parameters of the difference, are unknown, and no information is available by which they can be calculated.

The daily calorific requirements of kushta otters in the wild would be higher than those of Harris's specimens. Harris's

figures, in consequence, represent only an index of the minimum daily food intake for animals of a specific (unknown) weight.

There are other factors which qualify this index value. Much of the processed food Harris fed his specimens is enriched, relative to wild foods, by the addition of supplemental nutrients in high concentrations. There is little or none of the shell, tendon, skin, etc., which is ingested by predators along with the meat.

The meat of domestic animals produced by modern animal husbandry is richer in fat content, vitamins, and minerals than that of average mammals in the wild state. Relative to the otters' daily requirements of these materials, commercial meat would provide more of such minima per unit weight than much of the meat obtained by predation.

The thermal regime experienced by kushta otters around the year is equivalent to that experienced by most inland otters during the winter, only. Since otters must tread water to keep their heads extended while eating shrimp, shrimping involves more energy output per unit capture effort than do fish or crab catches. Energy requirements per unit biomass are consequently very much greater for active sea fishers than for captive otters.

In the absence of any specific figure useful for kushta otters, I will use Harris's index figure for daily food consumption as an index of the relationship between time and foraging activities in one selected pod, that of Goose Cove, for

summer, 1978. The organisms most frequently taken during this summer were king crabs, pink shrimp, and Dolly Vardens. There are only limited data on the weights and other population parameters of these species from Glacier Bay itself, or no farther away than Icy Strait, in the research reports.

I expect that kits would require a larger protein intake, proportional to body weight, than would adults. On the average, the amount of scat deposited by the kits is about half that of the adults, volumetrically. The kits' success ratio in shrimping is less than that of adults.

The female was still providing the kits with fish late in the summer. This fact indicates that she spends more of her time foraging than is required for her personal needs, even after the kits have begun to forage for themselves. The female spent more time actively fishing in Goose Cove through the month of August than did either the male or the kits.

B. Pink Shrimp

Large samples of Pandalus borealis were collected from Glacier Bay for scientific study between 1951 and 1962. The number of shrimp in one kg of whole shrimp ranges from 145 to 189 individuals (Ellson and Livingstone 1952, Ronholt 1963). The weight range for individual shrimp is therefore between 5.3 g and 6.9 g per shrimp. The mean weight, 6.1 g, will be used here as the index animal, the ideal pink shrimp.

In Prince William Sound, 60% of the pink shrimp population sampled at the breeding season was immature, and of less than adult size (Feder and Paul 1977). The amplitude of shrimp sizes selected by otters is not known. The majority available to otters may be less than the adult mean in weight.

Success rates in shrimping dives in Goose Cove ranged from 70% to 88% (IV.5, below). The success rate of the longest uninterrupted shrimping session was 82% for the adults. This total of 38 dives by male and female yielded 31 with successful shrimp capture.

I suspect that only one shrimp can be caught or retained in the mouth at a time. Acoustic monitoring and other tests indicate that the shrimp in Goose Cove are too dispersed for otters to be likely to snap up more than one at a time.

Thirty-one dives would provide 189 g of whole ideal pink shrimp in 25.2 min. The strategy then yields 6.1 g of whole food biomass/27 sec dive (IV.5, below). At this rate, the ingestion of 1.36 kg of whole shrimp would require a total time investment of 3.02 hr per day. Even at the lowest observed rate of success, 70%, only 3.47 hr would be required for ingestion of the minimum weight. At this lowest observed success rate, 14.6% of the time of one day would meet the minimal food requirement.

If twenty-minute sessions are optimal for otters, ten twenty-minute periods, in the course of 24 hr, would be

sufficient to obtain the minimum food biomass from pink shrimp alone. But during shrimping dives, otters captured Dolly Vardens. Shrimping sessions so augmented would provide the minimum daily biomass in much less time.

C. King Crabs

The weight of a single king crab can not be estimated from a single carapace or leg shell, because weights vary between crabs of the same size, not only from sexual differences (females yield less meat per unit carapace width than males), but weights between males of the same carapace width at the same time of year also vary (Harrison et al. 1942).

The mean width of king crab carapaces left at feeding sites by Muir Inlet otters was 13.75 cm. Weights of crabs with such shells vary from 1.73 kg to 4.55 kg (Harrison et al. 1942).

On the average, the meat in the king crab comprises 23.5% of the total body weight. This meat is distributed at a ratio of 2:1 between legs:body. In crabs with 13.75-cm carapaces, the meat yield ranges from 0.41 kg (0.27 kg in legs, 0.14 kg in body) to 1.07 kg (0.71 kg legs, 0.35 kg body) (Harrison et al. 1942).

Since otters do not eat the viscera of king crabs, and invariably eat the leg meat and all meat inside the carapace, the percentage of body weight (23.5%) probably represents the exact amount ingested by the otter.

Parts of leg shell occur frequently in otter feeding sites and in scats, but pieces of carapace occur less frequently in either form. The meat of the legs is eaten in its entirety, and evidently is not separated from the shell. Sections of empty leg shells are found at feeding sites when there is no trace of the carapace. Legs may be removed from the cephalothorax and carried to feeding sites after the cephalothorax has been fed on. This may reflect the large sizes of many king crabs taken.

By Harris's index minimum, the largest of these crabs would provide about one meal each for two adult otters. The smallest crab would provide a single otter's one-meal limit. Since fragments of the same crab may be scattered through several adjacent feeding sites, each crab may be shared by the entire pod.

D. Dolly Varden

During salmon runs, otters take only small amounts of flesh from the bodies of large salmonids. Dolly Vardens taken alive during the summer are eaten entirely, except for the viscera, swim bladder system, gill arches, head, tail, and spine. Most ribs and smaller bones are ingested.

Muscle comprises from 50% to 60% of the body weight of salmonids (Lagler et al. 1977). The mean Dolly Varden taken by Glacier Bay otters, on the basis of measurements of skeletal remains I have found at feeding sites (III.1, above), weighs from 710 to 720 g. Such a fish provides from 355 g to 432 g of meat

per capture. This meat yield is the equivalent of three separate sessions of shrimp diving (allowing for shrimp shell weight.)

The largest Dolly Varden I found as otter prey originally weighed 2.46 kg, and yielded from 1.23 to 1.48 kg of edible meat. The median weight (1.35 kg) would supply both adults with their meal limit (0.45 kg) and leave 0.20 kg for each kit.

As I observed no difference in duration of the dives which brought up fish rather than shrimp, such a biomass represents a yield of 1.35 kg/27 sec dive.

Of all otter scats censused in Muir Inlet in summer, 1978, 22.6% contained fish remains. Such an incidence is disproportional to the total amount of fish biomass in the otters' diets, relative to remains of crustacean prey in scat. A much larger amount of meat is represented by a small amount of fish bones than that amount of meat represented by a number of shrimp shells in scat.

As many as 90% of the summer scats on the Pacific coast contained fish remains (Table 5). Otters obtaining such a high yield of meat need spend only a minimal amount of time per day foraging. Otters probably spend the smallest fraction of the annual activity budget in foraging when fish populations are high. When the fish yield is low, much more time must be expended in pursuit of prey. The surplus energy required for long-distance trips, swims, agonistic and other behaviour, would be most abundant during and after periods of optimal fish supply. This may be the determining point of litter dispersal (IV.2, below).

IV. DAILY ACTIVITIES AND INTERACTIONS

IV.1. CHARACTER OF DAILY ACTIVITIES

Some of the differences which purportedly distinguish Lutra lutra from L. canadensis seem in fact only to be responses to competition with human society. L. lutra is considered strictly nocturnal in its activities (Stephens 1957, Harris 1968, Erlinge 1969). My observations of L. canadensis indicate no bias toward levels of illumination. Activities of L. canadensis proceed at about the same frequency of time allotments night and day, winter and summer.

Liers (1951) found that the males of inland populations did most of their solitary travelling at night. This is also indicated by my observations; most of the solitary overland hunting around Thistle Cove was carried on at night. But single males have also been sighted in remote parts of the pod's range at any time of day (Streveler 1975, 1977), and I have found the males as often absent from the female and kits in daytime as at night.

This balance of diurnal-nocturnal activity is also reported for inland populations of L. canadensis (Grinnell et al. 1937; Liers 1951; Greer 1955; etc.). Grinnell observed a correlation between tide levels and the activity cycles of

maritime otters in California. Although it is possible that otters may pursue different prey relative to tide levels in some parts of southeastern Alaska (III.3, above), I have observed them active at all levels of the tide without any particular correlation.

Novikov (1956) concluded that cycles of diurnal illumination have far less influence on the activity of any carnivore species than does the proximity of human beings, and that carnivores may not respond to changes in seasonal illumination. Carnivores are usually active in the day time, in any area where there is no human competition.

I have found this to be true of all carnivores in areas which experienced no human activity other than my own unobtrusive presence. Other carnivores, such as wolves, marten, and mink, are susceptible to human competition in settled areas of Bartlett Cove and Gustavus, and are active at night in areas which none of the same mammals approach in the day time. This is not true of otters in those areas.

Kushta otters do not change their activity sites, even where human activities impinge upon their own. This is also indicated among Scottish otters (Elmhirst 1938). The frequency and timing of the otters' activity periods, however, may be modified. Otters are usually displaced from their focal waters by the entry of motor boats, sea planes, and, where applicable, by motor vehicles. As the animals in Goose Cove were accustomed to

inboard-outboard patrol boats moving in and out of their focal water, and to large ships passing in Muir Inlet outside their cove, it is significant that the otters were displaced from the water much faster, and exhibited more alarm, at the low overflight of an airplane than at the approach of any boat. Either the volume, frequency, or novelty of the noise may be the major alarm stimulus to the otters.

None of these otters are disturbed by the approach of one human observer, walking, in a kayak, or in a canoe. None of these otters have become nocturnal on account of human activity, not even in Bartlett Cove, where the resident pod experiences human proximity daily, year-round.

Sea otters are also equally active day and night, only females with kits showing any bias toward nocturnal foraging (Shimek and Monk 1977). Even that may be due to the nocturnal availability of certain prey items.

Inland otter pods are said not to be active in daily interassociation for the majority of the total annual activity budget (Stephens 1957, Harris 1968, Erlinge 1969). There is some consistent pod association among some inland pods, however. The male remains with the family for at least a part of the time, and participates in the training of the kits, in pods in California (Grinnell et al. 1937), Siberia (Novikov 1956), and Sweden (Erlinge 1969). The percentage of the pods in inland ranges which remain associated consistently, as opposed to those which are usually segregated sexually, is unknown. Consistent pod association must

be facultative in inland pods. The same trait is positively selected for in maritime habitats (below).

That Lutra lutra breeds at any time of year, without a specific season, is considered by Stephens (1957) a further response to human competition. Neither Stephens nor Maxwell (1960) found any evidence of consistent breeding in any British otter population. But statements in Elmhirst (1938) and Barrett-Hamilton (1912) certainly lend themselves to the interpretation that a specific breeding season existed for the kushta otters on the northern coasts of Ireland and Scotland. Both authors assume that parturition occurred in late winter or early spring, and that the annual migratory activities of these otters were timed to coincide with arrival at the seacoast in that season for the specific purpose of breeding.

Erlinge (1968, 1969) found that Swedish otters bred and bore young almost any time of year. Novikov (1956) questioned whether this was true of populations in remote wilderness.

By contrast, there is no evidence for out-of-season breeding by L. canadensis. Among kushta otters, such predictability of breeding season is in keeping with the annual consistency of range use, food habits, and other activities. The same seasonality is also true of inland American otters, despite the more frequent dissociation of pods. This dissociation, and the tendency to wander more widely in disparate territories, is a trait which inland American otters share with inland L. lutra (Stephens 1957, Erlinge 1968, 1969).

Evidently there are features in common between the two species of kushta otters, and that such features distinguish the kushta otters of both species from the inland populations of both species. Such features must represent common denominators of the selective pressures related to the maritime environment.

Activities described in this section may not be comparable to activities of inland otters. The chief distinction is that the male of kushta pods is usually present with the female and kits on a daily basis.

For the purposes of this discussion, I will classify all activities of the daily and annual activity cycles of kushta otters under five headings.

(1) Interactions with prey species (foraging). These activities include diving, bottom hunting, pursuit of nektic prey, possible pursuit of surface prey from underwater, shore hunting and scavenging, overland hunting, and "semidiving" for mollusc extraction (IV.5, below). The degrees of frequency of these activities change from season to season, and differ from pod to pod, dependent upon terrain and the cyclicity of preferred prey. Despite the importance of this set of activities, some of the time included under the heading does not include actual predation. The majority of the time spent on shore and tracking overland, at least in winter, does not result in any food yield.

Foraging activities were discussed in detail in III.2, above.

(2) Interactions with non-prey species: predators, competitors, intruders. For some pods this is a null set. For most, it is an insignificant part of the daily, and even the annual, activity budget. For the Goose and Barco pods, this factor becomes significant in shaping the daily activity budget.

The Goose pod was frequently displaced from its foraging activity by the passage of boats or planes, or the entry of motor boats into its focal water. In most cases the displacements were brief. The otters returned to the water as soon as the intrusion passed, or the motors of boats coming into the cove were shut off. The otters were not displaced by noiseless boats, or by human activity.

The periods these otters spend on shore, or on their ledge, during such displacements can not be classified as resting. From the speed and immediacy with which these otters returned to the water as soon as the disturbance had passed, it is evident that the wait on the otters' part is an impatient one. Such waits do not involve any bodily relaxation, but constitute an alert vigil. Such periods can not be classified as resting behaviour.

(3) Intraspecific interactions. The relationships between members of a pod, not principally directed toward any other activity: adult-adult, adult-kit, and kit-kit interactions. Apart from foraging, these involve relatively little time in the daily activity budget. Pod-pod interactions are too rare in this region to be rated at all.

Intraspecific interactions overlap with foraging activity when all members of the pod forage together. Both male and female also forage independently of the rest. The proportion of time spent in non-foraging intraspecific interactions would probably be higher if the activity of otters while concealed in their dens or ledges could be monitored steadily.

Agonistic activity should be included in this category, but such activities seem to be much less frequent among kushta otters than among inland otters (Liers 1951, 1953; Cahalane 1947). Solitary play comes under the following heading.

Vocalisations are not entirely intraspecific in character. As activities, some vocalisations belong to interactions with non-prey species, above. Intrafamilial interactions are dis,ussed in IV.2, below. Vocalisations are treated as a special case in IV.3, below.

(4) Substrate-specific interactions. Swimming and overland tracking overlap substantially with foraging activity. Much of the winter cliff and rock climbing, tree scrambling, play on ice and icebergs, etc., seems to be independent of foraging, but this may not be the object on the otters' part. There may be an impulse toward territorial maintenance underlying some of these activities. Such an activity as the 90-m cliff climb by the Boussole male overlaps with foraging activity in the summer, but not in the winter.

Details of special cases of substrate-specific behaviour which does not overlap with other activities are discussed in IV.4, below. Diving and swimming, as a special case, is discussed in IV.5, below.

(5) Resting. Liers (1951) found that his otters slept about half of their time, winter and summer. The "naps" average two hours, and the otters usually slept for that time around noon. Solf (1972) makes the same statement, but may be quoting Liers rather than reporting first-hand observations of kushta otters in Prince William Sound.

I can affirm that otters are out of sight, either in dens or other retreats, for at least half of the time in any given sample of observation periods, winter or summer. I can not confirm that the otters are sleeping for any specific portion of this time. Sleeping is only one component of the category of resting. Digesting and excreting are resting activities during which the otters are not sleeping.

Periods of interaction between the male and female after a session of dives, are resting activities, but are a case of intraspecific interactions and are so treated in this study.

Evidently the female and kits sleep in dens during winter. The male may not always do so. I have observations of the male's sleeping apart in one-time-only shelters (II.2, above).

In August, the Goose pod slept on the habitual resting ledge. The pod evidently slept only when the male was

present. When the male was absent, the female and kits were always visible in some other form of activity.

In Thistle Cove in winter, the female and kits were inactive when the male was roaming by night.

On 22 August 1978, I observed the Goose adults spend 25.2 min shrimping in the cove, as already described (III.3, above). At 1558 hr, foraging activity was terminated voluntarily, due to satiety. After several minutes of mutual muzzle contact by the male and female on shore, all four otters went up to the habitual ledge, concealed by vegetation. The cove and all approaches were kept under observation. The pod did not return to the water until 2030 hr. One hour of the intervening time was required to digest the entire stomachful of shrimp. For the remaining 3 hr 30 min the adults were postdigestive and inactive. For 18.75% of their total day, adults and kits remained in unbroken resting activity.

IV.2. INTRASPECIFIC INTERACTIONS

A. Pod Structure

Kushta pods are active in interassociation more of the time than are inland pods. An additional difference between kushta and inland otters lies in the tendency of the kushta kits to remain with their parents for two years, and possibly more, after birth.

Inland otter pods, evidently with few exceptions, tend to disperse after the first year (Erlinge 1968). Among kushta otters even the birth of a new litter does not lead to dispersal of the older litter. Several of the pod counts in Table 14 indicate that the pod, in the second summer of one litter's life, contained two or three new kits. In Goose Cove, 1978, the two kits were a year apart in age (unless the smaller one was pathologically stunted). The same litters of both of the pods studied on the Pacific coasts remained intact for two years, and were observed to increase the second summer. All the previous litter of three remained with the Thistle pod after the birth of two new kits, spring, 1975 (Streveler 1977).

I know of no sightings which indicate that any adults in an established pod range ever passed a year without any kits. The lowest number for one year's litter is that of one kit (Goose pod, 1969). But although one first-year kit was

observed with the same pod in summer, 1978, one kit had been lost earlier in the summer. This same pod seems to undergo an exceptional degree of population turnover, and is a poor index of litter size.

Other sightings indicate that litters average two or three per year (Table 14). A pod may consist entirely of first-year kits with adults; of both first and second-year kits; or entirely of second-year kits, and perhaps even older sibs. No otters are likely to breed every year (Stephens 1957, Harris 1968), but if the kits in Goose Cove in 1978 were only a year apart in age, as they seem, breeding may occur more frequently, and perhaps annually, when the rate of population turnover is higher than it seems to be in Bartlett Cove or on the Pacific coast. Reproduction among other carnivores is accelerated in such cases, and may be among otters.

There are three components of any kushta pod. (1) A pair of adults, which are mated for long terms, but possibly not for life. Liers (1951) observed among his tame otters some shifting of mate allegiances, not consequential to loss of mates from mortality. As some of Liers' males were still breeding at 12 years of age, the duration of breeding life may exceed the total period of mate association.

(2) The elder kits, two, or possibly three, years old, which continue to associate with their parents at least for the first summer of the successive litter's life. (3) Evidently the

first-year kits never leave their parents voluntarily; only after the second summer do litters disperse.

As will be detailed below, there are behavioural distinctions between the first- and second-year kits. The second-year animals are more independent of the adults than are the first-year kits.

B. Reproductive Season

I observed three kits both winters of my study in Thistle Cove. These were the same animals. No members of the previous litter had remained with this litter into the first winter of its life. This litter, in turn, was observed during summer, 1975, with two new kits (Streveler 1977).

The suggestion is that the older brood would probably depart from its parents in the autumn of the year, concomitant with the energy influx from the spawning run of salmonids. Since I did not observe the first Thistle litter for the first time until November, 1973, such a departure by the older brood could already have occurred.

Parturition in American otters takes place in either March or April, and rarely as late as May (Liers 1951, Hamilton and Eadie 1964). Hamilton and Eadie found that the testis of the male otters regresses after March or April. Foetal development was completed in two or three months. Since they, and Liers, found

that otters breed shortly after parturition, with a resulting gestation period anywhere from 9 mo 18 dy to 12 mo 15 dy (and this in the same female ((Liers 1951))), all concluded that implantation was delayed as much as eight months. This reproductive strategy is facultative among mustelids generally, but is evidently lost in Eurasian Lutra lutra.

The male's testes begin to descend in November. Females are in heat from December to April. Breeding is almost always in March or April (Liers 1951). Male otters first produce sperm at the age of two (Hamilton and Eadie 1964), and females first breed at the same age. Liers did observe one female breed as early as 1 year, 3 mo of age.

Otters are ready to mate at the age of two, but Liers found that younger males were not successful breeders until they were five or six years old. In Liers' studies, younger males were directly associated with competitive older males. His observation may not be applicable to wild populations. Since the kits in wild pods disperse from their parents after the age of two, the onset of puberty appears to be the factor which initiates dispersal from the natal pod. All observers have found that males tend to roam much more widely during the breeding season (Liers 1951).

All kits in Glacier Bay pods have been first observed at the beginning of summer. On 16 May 1970, there was a unique observation of a female at Goose Cove whose teat distention

indicated ongoing lactation (Wik's log). Kits too young to move away from the den were found by miners along Nunatak Creek, in Nunatak Cove, in mid-May, 1969 (Cornelius's log). Inland kits are not allowed outside the den until they are 10 to 12 weeks old, although they cease to be "helpless" after the sixth week from birth (Liers 1951).

I was present in Thistle Cove until 9 May, 1975, and saw no new kits. However, the otters were absent more often during the month of April than they had been at any earlier period. That summer, two new kits were observed (Streveler 1977).

On this slender evidence, it appears that kushta otters are born in March or April, are retained in the den until the end of May (still nursing), and become able to forage for themselves in June. This is consistent with reports for all populations of L. canadensis.

By June, the new brood is able to forage for itself or to begin learning to do so. By July, kits are sharing all parental foraging modes, except that of overland hunting. Even in August, the female was still delivering food to the kits on occasion.

The parents supplement the kits' diets through the summer, but I have no evidence that they do so in winter. In winter, all the kits I observed were with the parents in the water at the same time, and never confined to shore for any purpose while the adults were foraging. Such confinement to the shore occurs

occasionally in the summer.

Second-year kits are more independent of the adults, and sometimes move alone in water or on land. First-year kits do not exhibit this independence of the adults. One second-year kit in Thistle Cove swam as much as 18 m behind the rest of the pod. I sometimes saw this kit in the north end of the cove when the rest of the pod was out of sight.

In Goose Cove, I twice saw the older kit, in response to its mother's alarm signal, run up the beach, passing within 5 m of me, and take shelter in the alder refuge site behind me. Both times, its mother and younger sib went into the water together.

C. Litter Sizes

Hatler (pers. comm.) observed the following distribution of litter sizes among kushta otters on the west coast of Vancouver Island. His counts do not distinguish between first year, second year, or composite litters. As an index of Pacific coast pod litter sizes, these figures offer a basis for comparison with Table 14.

Litter size	1	2	3	4	5	6
No. of litters of that size observed	1	3	11	5	1	2

TABLE 14. FAMILY SIZES OBSERVED IN OTTER PODS IN GLACIER BAY AND OTHER LOCALITIES IN SOUTHEASTERN ALASKA

Sources cited in text

Locality	Summer	Winter
Bartlett Cove, 1960		2 adults, 3 kits
Bartlett Cove, 1967		2 adults, 2 kits
Bartlett Cove, 1970	2 adults, 2 kits	
Bartlett Cove, 1977-78		2 adults, 4 kits
Goose Cove, 1969	2 adults, 1 kit	
	2 adults, 2 kits visiting[1]	
Goose Cove, 1971	2 adults, 5 kits	
Goose Cove, 1974	2 adults, 5 kits	
Goose Cove, 1975	2 adults, 2 kits[2]	
Goose Cove, 1977	2 adults, 4 kits	
Goose Cove, 1978	2 adults, 3 kits[3]	
Rowlee Point, 1968	2 adults, 2 kits	
Boussole pod, 1973-74		2 adults, 4 kits
Boussole pod, 1974	2 adults, 4 kits	
Boussole pod, 1974-75		2 adults, 4 kits
Boussole pod, 1975	2 adults, 4 kits	
Palma Bay, 1974	2 adults, 3 kits	
Thistle Cove, 1973-74		2 adults, 3 kits
Thistle Cove, 1974	2 adults, 3 kits	
Thistle Cove, 1974-75		2 adults, 3 kits
Thistle Cove, 1975	2 adults, 5 kits	
Sitka Narrows, 1975		2 adults, 4 kits
Garforth Island, 1977	2 adults, 4 kits	

[1]Some newborn kits, number not given, had been seen in Nunatak Cove in spring of this year. This Nunatak Cove pod may have been the visitor.

[2]This pod included the blond female, present only for one summer, 1975. Both these kits were first-year animals.

[3]One of three kits observed in early June, 1978, had disappeared by the middle of June. Of the two kits remaining, one was a first-year, and the other a second-year, animal.

Two and three kits have been observed in same-year litters in Glacier Bay. The four winter kits in Bartlett Cove in winter, 1977-78, were the same age, given the lack of variation in their size and behaviour. Observations of five kits in any Glacier Bay pod have been made only for pods in which first-hand monitoring documented composite litters.

D. Population Turnover

It is difficult to determine the age of otters from teeth or other anatomical criteria (Stephens 1957). The longest lifespan for an individual of Lutra canadensis was 21 years; this animal was a pet (Liers 1951). The longest-lived Lutra lutra was 22; this animal was in a zoo (Simon 1943). Fourteen-year lifespans are considered feasible for wild L. canadensis (Ingles 1965). Males have been observed still breeding at the age of 12 (Liers 1951).

The persistence and stability of a pod within a specific territory exceeds that of the pod's members. Because of the uniformity of size and colour among kushta otters, it is impossible to determine from observation alone how long single individuals remain in residence in any one group.

One set of observations indicate that three different females inhabited Goose Cove in three successive years. A blond female observed in the cove in summer, 1975, was a different individual from the dark females of the previous and subsequent summers (Nigro's log). Each of these females had litters,

but the litter of the blond female, two kits, indicates no carry-over from the previous year.

The 1974 female had five kits, which strongly suggests that the same individual had been present at least one previous summer. Unfortunately the log entry for the 1976 litter count has not been found. The 1977 litter, four kits, suggests a composite brood, but could be a single-year litter.

Since both kits observed with the blond female were dark, they could not have been differentiated from a litter born to another female. A female only newly mated to the same resident male might inherit the litter of a previous female, if this predecessor had been lost to mortality. There is no way to establish whether the male was the same individual throughout this time.

The record of one kit in Goose Cove through the summer of 1969, and again in 1978, when only one survived (another was lost earlier in the summer), suggest that there is loss from initially larger litters in this cove. Population turnover among kits and adults seems high in the Goose pod, compared to any others of long-term record.

These changes may not reflect remating, but rather resettlement by newly mated pairs. This may be a characteristic of glacially newly-opened territories; it may be an association with predation factors associated with the proximity of a large breeding seal population (V.1, below). There are no indications of similar turnover in Bartlett Cove or the Pacific coastal pods.

The occurrence of a resident otter pod in Nunatak Cove in 1967 and 1969 indicates that this is the only territory from which an otter pod, documented at one time, disappeared completely. The proximity of Nunatak Cove to Goose Cove is suggestive of problems of population maintenance generally in this periglacial area. Whatever brought about the abandonment of Nunatak Cove seems also to prevent reestablishment of otters there.

E. Whole-Pod Interactions

When the kits and adults are on shore together, but out of sight of each other, association is evidenced by the fact that acoustic contact is substituted for optical contact between the separated groups.

When the Goose pod kits were in dense growth below the feeding ledge, the adults made a snuffling sound as long as the kits were out of sight (IV.3, below). If the kits were romping over the cliff or along the shore, and dislodged or rattled loose rocks, the adults did not make any sounds.

When any pod entered the pod together, the male invariably went first. The female followed, and the kits followed her, either singly, or as a group. The male was usually the first to leave the water. On occasions, when the male perceived a threat to the pod, he left the water first, and then turned at the water line to "cover" to evacuation of the rest. Then he followed them up the rock. Otherwise, the male leads the pod

out of the water and remains in front.

When the Thistle pod swam together, the adults swam almost abreast in the lead. The male swam slightly in advance of the female, and elevated his head above the level of her head. When all the kits were second-year animals, this pod did not necessarily swim in close association.

When the kits did follow the adults, the kits either swam side by side, abreast; or two swam abreast, and the third behind; or all three swam single file. On rare occasions, the entire pod swam single file, the male in the lead, female second, and kits behind. There did not seem to be any determinism in the positioning of individual kits relative to each other.

The Goose pod went up the rock face to its ledge single file. Any pod crossing rock or gravel beach tended to do so single file, or in a huddle.

In Thistle Cove, the female usually swam on the side near the shore, and the male farthest from it. The male's position was determined relative to the proximity of the shore, and not to the female. She swam to his left when the two swam north, and to his right when they swam south.

The Boussole pod exhibited the same formation when swimming up and down the Yay River. The male led, the female beside or behind him, and the kits followed with no particular pattern. John Rose and Ed Murrell (Wildlife and Fisheries Program, University of Alaska, pers. comm.) observed the male come ashore at times,

leaving the rest of the pod in the water. Every time the pod swam up or down the river and encountered a fish weir these men had constructed, the male reached forward with its paws and with one or two thrusts separated the wood and wire. Then the male moved through the break. The rest swam or clambered over its remains and resumed formation behind him.

On one occasion in Goose Cove, my kayak drifted among the pod while it was shrimping immediately below its habitual resting ledge. I knew that if I raised my paddle and changed course abruptly the otters would be displaced, so I allowed the kayak to drift. The drift was slow. Not until I reached the limit of the water area in which all four otters were diving, within 2.5 m of either adult, did the pod turn and swarm ashore, although it had been aware of my presence and direction for several minutes.

I immediately swung around and paddled back to mid-cove. As soon as I had turned, the pod came back down the rock single file, male first, and entered the water. But as soon as the kits entered the water, the female swung her head toward them. The two kits returned to shore and remained there, at the water line, for the remaining twenty-five minute session of diving by the adults.

I once walked around a high rock at the north end of Thistle Cove and encountered the pod just 12 m from shore. The male swam toward me, 15 m in front of the female, while she remained where first seen, the kits around her. She watched as the male came within 12 m of me and delivered several snorts

(IV.3, below). Without any haste, he turned and swam back to the female, and the pod went southward at usual speed.

In October, 1975, four people encountered an otter pod on a gravel bar in Gustavus. The male snorted at them and then charged up the bank toward the observers, coming within 7.5 m of them. They did not move. The male returned to the family, which had not changed position, and herded them back to the water (Rita Wilson, Gustavus, Ak., pers. comm.).

I made no sightings of an entire pod on sand beaches, because pods rarely appear there. The superposition of tracks where the Thistle pod crossed Dixon beach, or the Boussole pod crossed Boussole beach, indicated that both adults were walking abreast, and the kits followed, either abreast, or in an unstructured huddle, as when swimming. On less commonly used beaches, the pod sometimes moved single file.

The Barco pod crossed pan ice in Bartlett Cove in single file, the male in the lead, testing the ice with each step. Streveler has seen kits eating prey on the ice in Bartlett Cove, when the adults were out of sight. No one has recorded seeing a kit eat on shore when the adults were out of sight.

No observation of mine will support Solf's (1972) contention that the female dominates the pod. The female naturally determines the activities of the kits when the male is absent. When the male is present, he determines the type and direction of all activities, and the response, including hers,

to all stimuli. When the male is absent, the female's responses and judgements duplicate his, except that she never leaves the kits to challenge intruders. Her dependence upon the male's decisions appears to be total.

Whenever I approached or peered into an occupied otter den, the male's face was the only one which confronted me.

Since mink never enter the water for more than a single brief dive, otters are the smallest habitually seagoing mammals on the Alaskan coast. Consistent pod association is probably selected for as a response to this fact. The selective value of such continual association among inland populations is less obvious, and less often observed. When the earliest evolving Lutra otters arrived at the seashore, phocids and otariids were already common there.

A degree of competition, or of inhibition of habitat exploitation, on the part of the otters, is occasioned by the appearance of harbour seals in the otters' focal waters. The presentation image of an entire otter pod moving together provides visual impact to aquatic competitors out of proportion to the size of one otter.

As a rule, harbour seals in Glacier Bay do not move in groups. Groups of seals sometimes congregate in sheltered waters, but do not move over distances in association. A presentation image with greater dimensions than the silhouette of a single otter may have a positively reinforcing effect in

deflecting other species' competitive or displacement attempts. Habitually solitary animals would not be so reinforced.

Given the close association of all swimming otters relative to any similar group of phocids, the presentation image of an otter pod is much larger than that observed by seals or sea lions among themselves.

I have seen single otters in waters as much as 5 km from shore, where harbour seals, sea lions, humpback and killer whales were active at other times. But sightings of solitary animals there were rare, compared with the number of sightings of associated pods near shore.

This tendency to association may represent a stage essential to the course of marine adaptation. Solf (1972) reported super-pod groups in Prince William Sound, in which several individuals of the same sex or age formed small rafts while moving through marine waters. Such enlarged pod groups may be generated by the infrequent occurrence of "visiting" among otter pods (II.1, above). The factors which select consistent associations among pods may function to develop superpod aggregations with ever larger presentation images. These would lead to culmination in the formation of large rafts of multi-pod character; such rafts characterise marine populations of the chungungo (Simon 1966) and the sea otter (Kenyon 1969).

I have not seen a single file of otters porpoising through the water. Hatler (pers. comm.) reports this spectacle as frequent west of Vancouver Island, and near Vargas Island. He believes that many supposedly well-authenticated "sea serpent" sightings have their origin in observations of this expression of otter behaviour. Although such behaviour may be playful in origin, the resulting image would strongly reinforce the large presentation image of a pod with a movement definitely designed to provoke xenophoby in competitors. Such behaviour would then be selected for as an influence deflecting possible competition or predation by other marine mammals.

F. Adult-adult Interactions

When the pod is together, all observed interactions between the adults are directed toward monitoring or training the kits, or toward whole-pod behaviour. It is only when the adults are resting together on land that interactions specific to themselves are observed. On the basis of daily observation, the total time expended on these activities amounts to ten or fifteen minutes. There may be more interactions when the otters are in shelter.

After a shrimping session, the Goose pod adults were resting together at the edge of the water. The kits had gone up to the ledge. The pair spent ten or twelve minutes in facial nuzzling. The male rubbed his muzzle against the muzzle,

chin, and the top of his partner's head. She responded with the same movements. Sometimes this rubbing was extended over her head and neck. I observed no oral or muzzle contact posterior to the shoulder of either partner.

This activity was muzzle contact, not contact with the rest of the body. It is not any form of grooming. Stimulation of the vibrissae is the object, as it is to these hairs that each otter returns its mouth again and again in the course of rubbing.

The vibrissae are the most tactually sensitive part of any otter's body. Close and repeated stimulation of each, by rubbing, seems to reinforce the pair-bond.

In Goose Cove, nuzzling sessions such as this were not interrupted by the disturbances which otherwise displaced the otters from the cove. I saw the pair interrupt such a session only once, when an iceberg overturned in the water. The sound of an overturning berg in Glacier Bay is associated with the churning up of shrimp in the water, and is a signal to begin foraging (for shrimp eaters). The otters had just finished feeding to satiety, and took no further notice, but returned to their nuzzling.

Such sessions occurred only after the completion of a foraging session. I saw no special interactions between the two when they reunited after separation.

G. Adult-kit Interactions

Adults determine the patterns and habits of behaviour entirely for the first-year kits, and to a large degree for the second-year kits. The kits' bonds of association with the adults begin to weaken late in the second summer. These bonds have begun to break in the second winter, when the kits may sometimes be active entirely by themselves.

When the male is absent, the female leads the kits in swimming, taking the position which the male usually assumes. She precedes the kits entering and leaving the water.

Above water, the female communicates her warnings to the kits without vocalisations. To warn the kits to return to land once they had entered the water, she tossed her head once over her right shoulder, facing away from the nearest shore. The kits returned to land at once.

On two occasions in late August (III.2, above), the female was in a mussel bed in Goose Cove when she suddenly became aware that I was sitting on the beach 25 m away, watching her. She had already been struggling in the mussel bed for fifteen minutes. On both occasions, her turn toward me as sudden and was followed by a whole-body spasm, identical with the "jump" of a startled human being. The younger kit immediately went into the water, and she followed him. The older kit ran up the beach along an established escape route. This route passed within 5 m of my position, and so did he. Both kits made

the same response on both occasions, initiated by her whole-body spasm.

The female vocalises continuously underwater when she is diving with the kits (IV.3, below). Inland otters vocalise steadily while training their kits for overland hunting (Liers 1951). I have not heard any otter female make an aerial sound.

When the female and kits rest together on the shore, she sometimes nuzzles their noses, or moves her mouth or muzzle around their own muzzles, or the tops of their heads. As with adults, this attention is concentrated on the muzzle.

This stimulation of the vibrissae of one or both otters by the others suggests that this nuzzling is a major communicative interaction which reinforces intraspecific bonds among otters and, continued into adulthood, reinforces the pair-bond.

The noses of otters are especially sensitive because of the vibrissae. Liers (1951) observed that the female nipped the noses of kits in the course of training them. The kits are said to tug the male's vibrissae with their teeth when they are small.

The kits accept the adult's judgements in regard to the potential threat of intruders or disturbances. Like the adults, the kits show no further apprehension of, nor interest in, such intrusions. In this respect, otter kits have more

confidence in their parents' judgement than do the dependent young of any other mammal species of my observations.

H. Kit-kit Interactions

The kits of kushta pods do not engage in the jostling or interplay usually characteristic of young arctoids, at least in the wild (I have observed it in zoo specimens). This lack of interplay in the Goose pod, summer, 1978, may have been due to the age difference between the sibs. The tendency of the two to pursue different escape strategies suggests that their behavioural responses were already divergent.

When their mother took a fish to the kits on shore, the kits began eating the fish from opposite ends. This supports a likelihood of fairly frequent sharing of prey between them in early life, as suggested above (III.3, above).

IV.3. VOCALISATIONS

A. The Aerial Acoustic Environment

Savage (1957) believed that hearing was the otters' most important sense. If so, the habitual aerial silence which most otters maintain has survival value. On a monthly basis, such silence characterises all but a minute amount of their time. Except for wolves and red squirrels, the same is true of all other mammalian species in their common environment.

After fifteen years of continuous wilderness study in many parts of Alaska and North America, I must observe that accounts of laboratory investigation of mustelid vocalisations report more different types of sounds for each species than I have heard different incidences of any type of sound in the wild.

Racey and Cowan (1935) observed a female mink chirping to her kits while hunting. I have not encountered a female with kits, and solitary mink are silent. Gossow (1970) and Belan et al. (1978) report vocalisations of weasels and marten, acknowledging that more sounds are produced under laboratory conditions than are known from the wild.

Liers (1951) described five separate types of vocalisations among his free-roving pets: (1) chirps, (2) soft chuckles, (3) screams, (4) drawn out uh-huh, uh-huh, and (5) the female's caterwaul in copulation. He noted that chirps and chuckles were the most frequent sounds. I have not heard aerial

which could be described by any of these terms.

Liers also mentioned continuous, intensive vocalisation between a female and her kits while she was training them in terrestrial food-getting. I have no observations of such behaviour, but the female vocalises continuously when underwater with the kits. She probably does communicate with them in aerial training, but in the kushta habitus, aerial training is limited.

Seton (1910) added two other sounds to the otter vocabulary, but, again, these were heard only from a caged animal. Kenyon (1969), by contrast, listed nine highly diverse aerial vocalisations for sea otters. Most of these were heard from captive animals, or those in association with humans. They were characteristic of females with young.

The aerial acoustic environment is much the same on the Pacific coast and in Bartlett Cove. The interior of mature spruce forest is quietest. Fringe zones, especially at sea coasts, are somewhat noisier. Red squirrels chirp frequently in both. Their sound is similar to, but less varied than, underwater otter vocalisations. In winter, wolves howl, in concert or singly, about once a week in Thistle Cove, and at other sites along the Pacific coast. Birds, particularly chickadees and grosbeaks, are the major vocalists of the forest edge.

Passerines are rare in Muir Inlet. The raucous screams of gulls and terns are common. Wolf howls have not been

recorded by the resident rangers.

Mammal sounds in the aerial realm are infrequent.

B. Aerial Vocalisations

1. Snorting. Only the male otter administers loud, forceful expulsions of air through the nostrils when challenging a human intruder. When the male is in the water, the sound of his four or five snorts is punctuated by the patter of waterdrops blown from his vibrissae in the process.

I have heard these snortings only on one occasion in each of two pods. I have described the encounter with the pod at the north end of Thistle Cove, on 18 November 1974. The male made four evenly spaced, explosive snorts. At other times I surprised individual otters by coming abruptly around headlands. The only response was the noisy splash of a quick dive.

In 1978, the otters in Goose Cove adjusted to my presence quickly. Only when I allowed my kayak to float among them (18 August) did the male snort at me. After leaving the water, he turned at the water's edge and delivered one snort, as the female and kits started up the rock behind him. He followed them to the first ledge, turned, and snorted once again. Then he ran behind the others to the ledge, and turned, just before vanishing over its edge, to deliver one final snort.

In October, 1975, the male otter in Gustavus delivered an undisclosed number of snorts before charging some

human observers (Rita Wilson, Gustavus, Ak., pers. comm.).

Presumably no charge, false or real, would be undertaken without delivering snorts.

2. Snuffling. Snorts consist of expulsions of air. Snuffles seem to be produced by noisy inspirations. Long sequences of these sounds - quick, successive inspirations like those of an old hound sniffing over the ground, but louder, and without the hound's terminal snort - occur when adults are on land, and the kits are nearby, but out of the adults' view. As the kits were sometimes moving through weeds, so that their position was audible to their parents, the function of the snuffling may have been to keep them aware of their parents' location.

One instance of protracted snuffling followed the pod's enforced displacement from foraging dives because of the passage of a large, noisy steamer in Muir Inlet.

In 1969, NPS ranger Cornelius saw four otters in Goose Cove. One was eating a fish by the shore (it is not mentioned whether this was an adult or a kit). The other three began snuffling, at which the fish-eater looked up, spied the observer, and retreated. The fish-eater joined the other three on the ledge, and all four snuffled together.

There seems to be no threat component to this sound. It may represent an acoustic elaboration of the presentation image of the whole pod.

NPS ranger Ole Wik recorded a "low whuffling - nnnf nnnf" sound from two adults on the ledge in Goose Cove in 1971. He did not note whether the kits were present. The sound was loud - 3.20 am (Wik's log).

Only three instances of this behaviour were recorded at Goose Cove in summer, 1978.

3. Other sounds. In 1969, Cornelius heard "the high-pitched, bird-like call of an otter pup in the alders on the north side of Goose."

In 1971, Wik recorded a sound from the same two otters he had previously heard snuffling on the ledge - a "high, harsh aaah, aaah." Circumstances were not noted.

These seem to be true vocalisations. I have not heard them. The sounds I have heard are nasalisations.

C. The Submarine Acoustic Environment

In August, 1978, I was able to conduct a hydrophone survey of the submarine acoustic environment of Muir Inlet under contract with the National Park Service, with William S. Lawton (National Marine Fisheries Service, Marine Mammal Division, Seattle, Wash.). Lawton and I recorded all sounds of biological, glaciological, and technological origin. Motor craft sounds are heard frequently during the summer, and are propagated through the waters to a greater distance from their source than any biogenic

sound is. These man-made sounds provide a substantial disruption of the ambient sonic spectrum.

Compared to the early years of the 1970's, marine mammals, which were formerly numerous in Muir Inlet, have declined considerably in numbers and appearance frequencies. This fact had the compensatory advantage of eliminating any confusion as to the identity of the sources of those sounds we did audit and record; few candidates were in view.

Acoustically, the underwater realm is a sharp contrast to the nearly silent aerial environment. Submarine mammals and invertebrates emitted acoustic signatures every few minutes, the rates variable according to the species. Unlike the sonic spectrum of the Arctic Ocean, where each signature is continuous, with brief pauses, sonic signatures in the waters of southeastern Alaska are discontinuous and punctuational. There is much overlap of species and individual sonic signatures in the Arctic Ocean; there is no overlap between mammal species in Glacier Bay.

Harbour seals were the quietest of all species monitored in Glacier Bay, in sharp contrast to the echolocative ice seals of the Arctic. Harbour porpoises produced runs of clicks, and other phrases of limited variety. Orcinus orca, both male and female, were abundantly vocal, producing long runs of clicks, creaking-door wails, and other sounds, audible as far as 0.75 km

away from the mammal vocalising.

The commonest non-mammalian biogenic sounds are the snappings of pandalid shrimp. These occur steadily at intervals of 30 to 40 sec, and often more frequently.

Despite the murkiness of the water of Muir Inlet, it is evident, from the short duration and low frequency of production of these sounds, that none are echolocative in character.

Inside Goose Cove, the sounds of large ships passing out in Muir Inlet occasionally displaced diving otters back to the shore. Otters did not always respond to the submarine signatures of some vessels, even though the same signatures displaced otters from the water at other times. Other factors than sound alone were involved.

Otters in Arctic seas would be the least vocal of all mammals recorded there. In Glacier Bay, by contrast, otters are the noisiest mammals underwater, though only in one context.

D. Submarine Otter Vocalisations

Neither the male nor female otter, while swimming alone or together, produced any detectable sounds underwater. The sound of a tail switching through the water, or of feet patting the bottom, along with shrimp snappings, gave evidence that our equipment was functioning with its usual sensitivity at such times.

When all of the pod were diving together, there was an almost continuous, finch-like chirping throughout the duration of

the dives. These sounds began at the moment the diving session commenced, and were, with brief interruptions (4 sec maximum), almost continuous until the diving was concluded and the otters returned to shore. The underwater sounds continued if only one otter surfaced. If two or more otters surfaced, there was underwater silence until more than one of them was again submerged.

At least three otters were vocalising together, sometimes at the same moment. At least one of them was vocalising almost continuously. It is possible that there were four vocal components; only audio analysis of the tapes will reveal whether four different individuals were involved.

The contrast between one continuous, lower-pitched voice, and two discontinuous, higher-pitched voices, suggests that vocalisations were being produced by only the female and kits. All recordings were made during shrimping dives, so such vocalisations may be correlates of shrimping foraging, in the same way that aerial vocalisations correlate with training in overland foraging (Liers 1951).

On 15 August 1978, Lawton and I recorded almost twenty minutes of continuous otter vocalisations. At intervals, one or both of the higher-pitched voices ceased, and a single voice continued alone. The vocal continuum in its entirety was never broken for more than 4 sec. The kits' vocalisations evidently continued whether their mother was under the water with them or not.

These bird-like chirps began at a high pitch, and led into trills. The trills sometimes accelerated in speed, and runs of trills were heard. Such runs of trills lasted from 2 to 10 sec, with a maximum run (in one instance only) of 28 sec. Sudden high chirps broke in. Sometimes high chirps occurred after long, even runs of trills.

Discontinuous chirps occurred together with the snappings of shrimp, but without any correlation. Evidently the sounds elicit no response from the shrimp. The occurrence of shrimp sounds when otters are in the water is not different from those instances in which the otters are vocalising around them.

The same level of loudness was maintained throughout the vocalisations. The tonal range was not great - about equal to that of a flock of pine grosbeaks, though not so musical.

Analysis of the tapes by audio equipment not yet available may determine periodicities and other characters of individual vocal lines or voices, and apportion the vocalisations between separate individuals.

With or without the male, the female and kits are continuously vocal underwater. The female and kits together are the noisiest animals in the submarine environment of southeastern Alaska.

IV.4. SUBSTRATE-SPECIFIC INTERACTIONS

A. Tree-Scrambling

British otters climb trees (Millais 1905). The habit, though within the potential of all otters, has not been recorded by any American investigators.

One or more otters was consistent in the use of bridges formed by deadfall spruce over frozen watercourses in the Boussole Valley. Some bridges were 3.2 m above the frozen surface of a stream. In such cases, crossing these bridges saved considerable time otherwise required to move across the stream. The banks at those points were so steep that they were probably insurmountable when covered with snow.

These bridges were used otherwise only by the wolverine, red squirrels, and human investigators.

B. Cliff Climbing

Many records relating to the world's maritime otter populations assume a correlation between coastal rock faces, cliffs, and the incidence of otters (I.3, above). Such an association between sheer rock faces and Alaskan kushta otters is not invariable, but it is more frequent than association between otters and flat gravel shores (Table 3).

The Thistle pod climbed to heights of 15 to 18 m on nearly sheer gabbro cliffs at the east side of Dixon Harbor.

The same pod had a den on the summit of a 25 m cliff, on the west side of Dixon Harbour. This cliff was nearly sheer, and in winter, often coated with frozen spray. Only one animal climbed this cliff in the winter, and perhaps only one animal climbed around the frozen waterfalls on the east side of Dixon Harbour.

To the Boussole pod belonged the champion cliff-climber of them all. This otter climbed a 90 m cliff on the east wall of Boussole Valley an average of once a month each winter. The otter followed the course of the stream to the bottom of the cliff, kept reasonably close to the ice left by its descent up the nearly sheer face to the edge and crossed over to the surface of the pond. Parts of this ascent were often sheathed with thin ice.

The pond at the summit was frozen almost continually during the winter. The otter walked only short distances from the edge of the cliff over the ice of the pond, and returned back down the cliff. Once, the same otter climbed the regular trail about 40 m south of the cliff, but never otherwise made any other explorations along the cliff or the summit.

In summer, this pond contained sticklebacks and toad larvae. Jeff Skaflestad (Hoonah, Ak.) saw an otter in this pond several times during the summers of 1973 and 1974.

Undoubtedly the protection which cliffs and altars afford otters on the Alaskan coast reinforces the tendency to stay in practice by surmounting them under any conditions. To mount the sheerest of these, when no other mammal (except the wolverine) can do so, obviously has an adaptive advantage.

C. Ice and Snow Interactions

Otters rarely exhibit playful slides on snow during the winter in the Glacier Bay region. Such records are similarly rare for inland otters (Field 1970).

An element of play is usually involved in ice-oriented reactions. Otters often fall through holes in thin river or lagoon ice, and may attempt to climb back on the surface even while the ice continues breaking away beneath them. The Barco pod often sought to cross pan ice in the lagoon when the shore could be reached as easily without crossing any ice at all.

Icebergs are common in Muir Inlet and wash into Goose Cove on each tide. In summer, 1977, Zip Harrington (NPS, Gustavus) watched the six otters then resident climbing up and sliding down the sides of an unusually large iceberg beached in the cove (dimensions not given). Each otter slipped continually trying to get up the sides of the berg. None gave up until it had reached the top. This activity continued almost twenty minutes.

Like mink and weasels, otters tunnel into snow for short distances (1.2 m at most) during winter. Some of these tunnels may be for shelter. None seem to be directed to the pursuit of prey.

IV.5. SWIMMING AND DIVING

A. Swimming Habits

Positional relationships among the members of a pod swimming together were discussed in IV.2, above.

An otter swimming alone tends to keep a very low profile in the water. The head is kept submerged except for the nostrils and eyes, and intervening muzzle. The shoulder is usually visible. The remainder of the back and tail are not usually seen, unless the animal is swimming in the focal water.

When a pod swims together, the male makes a special effort to ride well above the surface of the water. Each winter morning, when the Thistle pod swam north into the cove, the male swam slightly forward of the female, and lifted his head entirely out of the water. His full back and most of his tail were visible. The female also lifted her head higher than she carried it when swimming alone, and most of her back was visible above water.

The kits made no effort to ride up in the water. When I saw one kit alone, this young otter usually kept its head completely out of water; when following the adults, the head was held low, the waterline just below the nostrils.

In Goose Cove, by contrast, the otters kept much the same profile whether swimming together as a pod, or swimming singly: the profile of solitary otters.

Otters are more buoyant in salt water than in fresh.

They float higher in the sea, unless attempting to maintain a low profile. When an otter pauses on the surface of the water, the entire body is buoyed up above the surface, as far as the midline of the abdomen, unless the animal is treading water to keep its body submerged.

When travelling overland, otters rarely pursue a straight line very far in any single direction. In the water, otters usually proceed straight from the point of entry to a point in the water at which diving begins. At the completion of a dive session, the otters swim directly back to the shore point where they leave the water.

Otters do not swim rapidly. I estimate the average swimming speed at 9 to 10 kph, the speed of a harbour seal moving slowly while watching an object of interest.

I have seen only one instance of a single otter "porpoising" in salt water. This animal was encountered 4 km southwest of Garforth Island on 22 July, 1970. At the approach of the motor boat, this animal, which was floating motionlessly in the water, leapt, dove for 6 sec, and reemerged. This otter was able to lift its body entirely out of the water from a stationary stance.

B. Swimming Distances

For otters, the maximum salt water swims on record are of 22.7 km, from Scotland to Ireland (Macintyre 1950), and of 24.3 km from the mainland to Vancouver Island in British Columbia

(Cowan and Guiguet 1973).

Gerald Thorne (Cordova, Alaska) saw a river otter 27.5 km southeast of Montague Island, south of Prince William Sound, in open ocean over a bottom more than 190 m deep (P. Mickelson, pers. comm.).

The greatest distance from the mainland that any Glacier Bay otter has been recorded is 5.2 km. Several individuals have been sighted on South Marble Island at widely separated times in the last decade. These otters live no nearer than the coast. To reach the island, these otters swim over bottoms deeper than 100 m, and through waters where humpback, Minke, and killer whales, as well as pinnipeds, forage actively.

But kushta otters rarely go farther than 0.4 km from the nearest shore. The majority of such otters spend their time within 150 m of the shore.

The otters seen near the face of Grand Pacific Glacier in summer, 1978 (II.1, above), were 20 km from the nearest inlet known to be occupied regularly by otters.

Otters are capable of travelling a linear distance of 405 m underwater without surfacing (Merriam 1884). Novikov (1956) considered L. lutra capable of moving 100 m in a single freshwater dive. The sea otter, by contrast, is recorded swimming a maximum underwater distance of 30 m, by an alarmed animal (Kenyon 1969).

I have observed a maximum underwater transit of 70 m, by a second-year kit, alone, in Thistle Cove, 27 January 1974.

In ordinary dives in Thistle or Goose Coves, the otters emerge near the point at which they submerge. I have observed displacements between the two of, at most, 12 to 13 m. Most of these displacements amount to 3 or 4 m.

C. Dive Types

Two types of otter dives were observed.

(1) Foraging dives. This is the most common type of dive. In an ordinary day, without disturbance from predators or competitors, 100% of all dives are foraging dives.

Foraging dives are characterised by the fact that the otters engaging in them spend more time underwater than in surface pauses, as adults (D, below).

Semidives (III.2, above) must be included in this category.

(2) Aversion dives. My one observation of a surprised young otter, above, can be considered an aversion dive. A kit in Bartlett Cove dove off the ice to escape a swooping eagle (V.1, below). Such dives are evidently rare on a seasonal or annual basis. The otters' customary response to a disturbance is to leave the water entirely.

D. Dive Depths

Otters have been taken, drowned, from crab pots at depths of 18.75 m, in channels around Sitka (Scheffer 1953).

Goose Cove is 10.6 m deep at mid-tide. At this tide level, with a hydrophone, I monitored a diving session of the female and heard what sounded like the patting of paws on bottom mud. Correlative acoustic evidence indicated that the otter was deep in the cove. This is thus the greatest depth documented for the otters in Glacier Bay.

USGS topographic maps of Muir Inlet (Fig. 7) define an 18.75 m contour line along the bottom around Sealer's Island. Otters dive in these waters in June and July and retrieve king crabs from the bottom (king crabs can not swim). It is possible that the otters are reaching depths of 18.75 m and greater, as they are capable of doing (Scheffer 1953, Maxwell 1960).

E. Dive Durations

As would be expected for a physically unspecialised mammal, river otters are not credited with any specific anatomical or vascular adaptations to diving. Lutra has no caval sphincter or hepatic sinus, and the onset of facultative bradycardia during dives is not only slower than that of phocids, but slower than in other aquatic mammals, such as the coypu (Myocastor coypus). After a 1.5 min dive, one otter's heart slowed from 260 to 42 beats/min

(Harrison and Tomlinson 1964).

From this experimental basis, a theoretical capacity for dives lasting seven to eight minutes has been calculated (Guenaux, in Hainard 1948). The maximum dive on record for Lutra is a six-minute immersion by a tame otter. The observer thought this could be exceeded (Maxwell 1960). The longest dive observed in the wild was one of 4 min 23 sec, by an otter fishing under winter ice in Michigan (Field 1970). The shortest dive observed by Field in this environment, 68 sec, exceeds the maximum submersion I have observed in Glacier Bay.

I recorded diving profiles for all of the Goose pod otters in shrimping sessions between 16 and 22 August 1978. I was able to record profiles at all tide levels. I found no detectable correlation between dive durations and tide levels.

Hatler (pers. comm.) recorded dives on the west coast of Vancouver Island. His maxima (40 sec), minima (11 sec), and mean (25.2 sec) dives are in accord with my own observations. Such dives must be representative of foraging activity along the Pacific seaboard.

When the male and female otter are diving together, there is initially a high degree of synchronisation: the female dives a second or two after the male's dive. This synchrony is lost early in the session, and is not resumed. When all four otters dive together, there is no synchrony between any individuals.

Surface rests are usually devoted to chewing shrimp, during shrimping sessions. This activity takes less time than catching one (Table 15). When there is no capture, the otter pauses only a few (less than 5) seconds at the surface and dives again.

The longest single set of dives I recorded lasted 25.2 min, and included 28 separate dives by male and female. Many shorter sessions were recorded. The mean dive, and the mean of surface pauses, indicate that more time is spent underwater (28 sec, or 56% of the cycle, by the male; 26 sec, or 58%, by the female) than on the surface (22 sec, or 44% of the cycle, by the male; 19 sec, or 42%, by the female) (Table 15).

When both kits are averaged together, the difference between dive durations and surface intervals is less than that for the adults. When one brief run by the younger kit was extracted from the common average, the youngest kit was found to spend more time on the surface than under water. This series for the youngest kit was recorded at 2130 hr, 21 August 1978. At this time, this kit spent 44% of its diving time underwater, and 56% on the surface. The performance of this kit's sib must be intermediate between that of the first-year kit, and that of the adults.

There may be a stress limit which restricts the length of shrimping or other diving sessions. The behaviour of the otters after the longest shrimping run I recorded indicated that the animals were relaxed and satiated.

In this session, the otters were in 5.75^{O} C water continually for 25.2 min, completely immersed for a total of 14.1 min. These conditions did not induce stress in the otters. The stress limit must be attained by values in excess of these.

TABLE 15. DIVING PROFILES FOR THE GOOSE POD, 16 - 22 AUGUST, 1978

Individual	No. of dives	Range of dive durations	Mean dive durations	Surfacing durations	Mean surface duration	%age time up/down[1]
Male	62	4 - 55 sec	28 sec	1 - 60 sec	22 sec	44% / 56%
Female	104	4 - 59 sec	26 sec	2 - 55 sec	19 sec	42% / 58%
Kits, together	59	3 - 35 sec	15 sec	3 - 55 sec	14 sec	48% / 52%
Youngest kit, alone	18	5 - 13 sec	8 sec	5 - 15 sec	10 sec	56% / 44%

[1]The percentage of time "up" is the percentage of the total time with head above the surface, out of the entire diving series. The percentage of time "down" is the percentage of the total time the otter was submerged during the over-all diving series.

V. INTERSPECIFIC INTERACTIONS

V.1. PREDATION ON OTTERS

On 30 January 1961, an otter kit was eating a fish on the pan ice in Bartlett Cove lagoon. A bald eagle stooped on it; the kit dove into the water (Streveler's log).

In two winters of study on the Pacific coast, I observed a single instance in which a bald eagle (the only large avian predator in the area) seized a mink from the snow and carried it off. An eagle made an attempt at another mink, which escaped. A fox was dropped from the air and recaptured without any wing marks appearing on the snow (Home 1977).

An Iraqi otter, relocated to Scotland, exhibited fear only of eagles. Eagles are predators on otters in Iraq (Maxwell 1960).

Eagles are predators on seal and sea otter pups in the Aleutians (Krog 1953, Murie 1959, Sherrod and Estes 1975). In late May and June each year, an average of 1,000 female harbour seals deliver pups on the ice floes in the northern extreme of Muir Inlet. Bald eagles have been seen eating dead pups at this time (Home 1973). No eagle has been observed killing a pup. There is mortality among pups for other reasons.

The rate of population turnover among the otters in Goose Cove, the pod located nearest the seal pupping-ice, is exceptional among pods studied (IV.1, above). A first-year kit disappeared from this cove in early June, 1978. In other summers, only one kit has been recorded there through the season. Litters of one are sufficiently rare (nonexistent in any other records in the Glacier Bay reserve) to suggest a possibility that other kits have been lost. Even the adult population exhibited a turnover of individuals distinct from any recorded elsewhere.

There is potential for predation on otters by eagles because there is so much overlap of the two species' habitual range and foraging activities. Eagles sit on rocks and trees overlooking all bodies of water in which otters are active. During eulachon runs in the Dixon River, which otters exploit, as many as 20 eagles congregate along the river (Home 1977). No kits disappeared during the period of these studies.

I found otter hair and bones in wolf scat on the banks of the Dixon River on two occasions, 9 January 1974, and 21 March 1974. No otters from the Thistle or Boussole pods had disappeared. These wolves exploited a total range 7x the length of the Boussole Bay/Dixon Harbour coastline. Several other otter pods were accessible to them.

This is not necessarily evidence for predation. The four wolves which hunted this marginal range were principally

beach scavengers during the winter. They did kill one young mountain goat each spring and fall, when goats crossed the valley floor.

These wolves also swam into the Dixon River during fish runs, and took fish of steelhead size on to the bank. A predatory encounter with an otter is not impossible.

Wolves, black bears, brown bears, and wolverines occur along all the beaches where otters occur, and represent possible predators. Otters which swim into the central waters of Glacier Bay cross waters frequented by killer whales at other times.

There may be predation on otters, but evidence is not available for anything but attempts. Rates of population attrition and turnover in Goose Cove, and possibly Nunatak Cove, indicate an impact on populations which has no parallel in other pods studied. Causes are unknown.

Tlinkit hunting and trapping activities have been carried out in Glacier Bay and the rest of the Alaskan coast for centuries (De Laguna 1972). Otters were being trapped around Lituya Bay in 1786 (LaPerouse 1799) and along the entire Pacific coast, before and after the extermination of the sea otter (Khlebnikov 1861). Intensive hunting and trapping in Northern Ireland has not produced any noticeable reduction in the numbers of maritime otters (Fairley 1972). Otters are still trapped everywhere in southeastern Alaska, except for Glacier Bay, where trapping has been illegal since 1938. There is no evidence that

otter populations are declining as a result of trapping (Alaska Department of Fish and Game 1977).

In 1977, Bob Johnson (Brownson Island, Ak.) informed me that he believed he had "trapped out" all the otters on the rocky south shore of Brownson Island. Because of the lack of any sheltered water body which could serve as a focal water, this area did not appear to be optimal otter habitat.

Mr. Johnson also trapped otters annually in the salt chuck system at the centre of the island. On the evidence of feeding sign and observations, otters were abundant there in summer, 1977. This area, by contrast, seemed to be optimal otter habitat.

Repopulation of sub-optimal habitat may proceed at slower rates, and be more sensitive to environmental impacts, than repopulation of optimal habitats.

VI. SUMMARY

Two objectives were pursued in this analysis. First, by literature review, I attempted to identify those special features which distinguish maritime populations of river otters, as a group, from inland populations of the same species. Second, I attempted to identify the factors which have been operative throughout evolutionary history to produce from otters and otter-like mammals (lutrines and lutromorphs) seal-like mammals increasingly adapted to exploitation of marine-oceanic resources, on the one hand, and generalised aquatic mammals, on the other, all positively selected for the retention of a conservative eurytopy. Such generalised lutrines have appeared recurrently in evolutionary history, coincident with increasingly aquatically-oriented forms which, ultimately, became modified somatically.

I found that both New World and Old World populations of maritime otters had several features in common, distinguishing them all, as group, from inland populations. Features common to all kushta populations (regardless of species assignment) include increased dependence upon a crustacean food base, with reduction of reliance upon mammalian, avian, and other terrestrial foods; larger body size; a generally darker colouration, with less variability of colour, and grizzling of the male's muzzle;

a lack of seasonal or migratory movements, and a greater conservatism of habits and range; the absence of markers along territorial boundaries, with a concentration of markers on sites of habitual use in the centre of most pods' ranges; a consistency of family interassociation (facultative in inland pods); and a regularity of breeding season in the spring (lost in L. lutra, but not in L. canadensis).

To test some of these findings, a study was devoted to comparison of the responses of four otter pods to four topographically, faunistically, and, in southeastern Alaska, biochronologically differentiated habitats.

The study of these kushta otters in southeastern Alaska evidenced three basic ecological modes in foraging and range activities determined by the geographical character of the home ranges. Such geographical features were more determinative of strategies than the factors related only to the biochronological ages of the habitats. Otters are highly adaptable, and have the ability to shape their individual and social existences around environmental variables to a degree greater than that of any other species in this environment.

I observed three ecological-evolutionary modes, parallelling those which have become fixed in the evolution of related lutromorphs in past epochs.

One, the "supermink," or terrestrial-freshwater hunting orientation, is evidently the most primitive ecological-

behavioural mode exercised by otters. Second, the "roensis" or generalised, amphibious exploitation of both terrestrial and marine resources to a degree of dependence determined by the relative wealth of resources in the focal water. Third, the "phocoid," or extreme-thalassotopic, strategy, oriented exclusively to the exploitation of marine resources, concomitant with a virtual abandonment of terrestrial foraging activities.

In this last mode, a point crucial to the abandonment of terrestrial dependence was seen in the necessary presence of slow-moving prey in marine waters of a size which could be captured and eaten in the water, without a return to shore or hard surface (e.g., shrimps, gunnels, etc.). The pod which had developed such wholly marine foraging also abandoned the use of dens (at least in summer), and exhibited no tendency to move inland even short distances, during the study period. In the evolution of seals, and of seal-like otters, from early lutrines, such a development must have determined the transformation of forelimbs to flippers.

Only one feature was found common to all pods studied: the focal water, a water body which is the centre of the majority of the pod's activities. This feature may be either salt or fresh water. Pod ranges are often (but not invariably) associated with rock faces, talus, gravel beaches, or boulders. Sand beaches were little exploited. Mud beaches were avoided.

Otters were oriented to rocks and cliffs chiefly because these features provided zones for foraging exploitation and refuge beyond the reach either of pinnipeds or other terrestrial carnivores. The ability to scale sheer cliffs has a protective function. In response to this, otters exhibited a tendency to climb cliffs even when they were sheer and covered with ice or frozen spray, to heights of 90 m, and to do so regularly.

Sites of habitual activity were alternated somewhat during a season, but such alternations sometimes consisted only of gradual movements of activity sites in a rotary way around the focal water. Changes in the activity sites of the otters were generally reflections of the changes in abundance and accessibility of the preferred prey. On a year-round basis, the pod occupied the focal water continually.

Neither dens nor elevated feeding sites (altars) were necessities within pod ranges, although such features were used by the otters whenever the terrain afforded them. Both dens and altars were sometimes left unused for long periods of time, even when the otters were active in the same area.

In two of these ecological modes ("roensis" and "phocoid"), otters tended to select sites on which they could concentrate their food remains and scat. Scat especially functioned as a territorial marker. Man-made structures were adopted and utilised as territorial sites, although elevated rocks were preferred. There was a tendency for the otters to expand scat

deposition sites around altars.

Otters responded negatively to the removal of their scats. Such acts were interpreted as an attempt to dislodge them from their territory. Otters abandoned use of sites from which their scats were removed, although they did not move from the territory. Otters may modify their activity patterns, but not their activities, in response to such changes.

The "supermink" strategy was concentrated in a freshwater system, involved more overland foraging, independent of watercourses, and more cliff climbing, than occurred in other modes. Habitual feeding sites, such as middens or altars, were not observed there. Random feeding sites were customary, especially along the river. This is also true of inland populations which exploit nutritionally marginal ranges (Field 1970).

The "supermink" pod was characterised by the fact that the adults spent a greater percentage of their time in independent foraging than did those of other pods. The adult pair sometimes abandoned the kits to forage together. The adults hunted overland, even during periods of low population density among small mammals.

The "roensis" mode was the most eurytopic of the three. Middens were fairly common, and altars were used whenever appropriate rocks were available. Middens accumulated on flat surfaces when elevated rocks were not available. These otters relied on terrestrial foods when they were available, and dispensed

with them when they were not. When terrestrial resources were in decline, these otters exploited marine prey to such a degree that the pod rarely came ashore, except to rest. Because of the prey preferred (crabs, fish), this mode required use of hard substrates for eating sites (rocks, pan ice).

The "phocoid" strategy was the most wholly marine-oriented. These otters abandoned use of land except for resting, and when feeding on king crabs. When these otters hunted shrimp, they consumed the prey in the water. This pod in Goose Cove made no use of a den (despite available structures), but only a resting ledge. It made no inland forays during summer. The otters made no effort to take birds and mammals as food, even though such prey were easily available around habitual eating sites. The male, in its solitary wanderings, moved only along the coast (to as much as 11.3 km from the pod), and not overland. Such pods did not develop any exploitation of new terrestrial resources as they became available by environmental succession, but did prey upon new entrants into the submarine fauna (urchins).

For the "roensis" and "phocoid" pods, random feeding sites were less common than habitual feeding sites, although more random eating was done in the water. Altars and more expanded sites, such as chancels, were preferred by these pods.

Kushta otters have become sufficiently adapted to the sea to swim as far as 27.5 km into open ocean from the nearest shore.

Near-shore zones remain the areas of greatest activity. Distant swims, rarely observed, may be characteristic of litter dispersal.

Otters show no apparent sensitivity to water temperature. None of the otters studied exhibited stress after swimming as much as 25 min in waters 5^{o} C. Some entered waters of 3^{o} C.

The diversity of the diets of each pod is a function of the diversity of available fauna. The habitats biochronologically oldest were associated with the most diverse fauna, and otters exhibited the greatest diversity of food items there. Even there, each pod evidenced a preference for one or two foods. Marine-oriented otters also had preferences among the available fauna in terms of the seasons in which such preferred prey were accessible.

In the diets of the pods studied, the preferred items were all crustaceans. Crab and shrimp predominated. Crabs were selected out of proportion to their biomass in the fauna, and crabs larger than average in the given population were taken selectively.

Foods other than crustaceans, including fish, seemed to be taken incidentally to the pursuit of Crustacea. Salmonids were taken by otters in much lower proportion to their occurrence. Otters elsewhere are said to be poor at catching the fast-moving salmonids, and to be dependent upon slower-moving fish. In all Glacier Bay pods together, salmonids constituted 80% of the fish taken. I suggest that visual cuing on the brightly-reflective bodies of salmonids in these turbid waters is the factor determining selective otter predation upon them.

The female and kits were active primarily in the focal water, and did not often venture elsewhere. The male may leave the female and kits unattended in the focal water, but rarely leaves them when all are outside the focal water. The range of the female and kits was usually 1/3 the area of the male's range, in three of the study pods.

Otters rarely vocalise above water. I discovered that the female and kits vocalise continuously when together underwater. The adults do not vocalise when both are diving.

Pair-bonds and family-bonds seem to be reinforced by mutual stimulation of the vibrissae. The male is the dominant member of the pod, and leads the pod when it is swimming or moving overland. He advances toward intruders and challenges them with nasal snorts. When the male is absent, the female duplicates his behaviour, but does not leave her kits to challenge an intruder.

The kits remain with their parents at least until the end of the second summer of their lives, even if a new litter is born in the meantime. Breeding may occur annually in some of these pods, especially where there is some litter attrition. No adult pairs have been observed to spend a year without kits.

A pod may have three components: the adults, mated for long terms; the first-year kits; and the second-year kits. The two groups of kits are differentiated in behaviour. First-year kits are completely dependent on the adults, and are still provided with food on occasion. Second-year kits exhibit some

independence, and may be active at times away from the rest of the pod.

Consistent pod association, which is facultative in inland pods, is selected for positively in the maritime environment. The male of maritime otter pods is absent from the pod less often than is reported among inland populations. There is no sexual segregation of dens in maritime otters, as there is among inland populations. I suggest that this is a development intermediate in the selection for large rafts of individuals, as observed in sea otters and chungungos. A selective advantage of this behaviour may be the enlargement of the presentation image. A single river otter is the smallest maritime mammal in Alaskan waters. A group image may help to discourage competition and predation. Otters respond negatively to the presence of harbour seals (or other marine mammals) in the focal water.

Pod association may reinforce the otters' ability to compete with larger marine mammals for exploitation of the same water range and the same prey base.

In any of these pods, "play" activities, such as sliding, are slight in evidence. Some playful behaviour is observed in the otters' interaction with ice.

Otters exhibit a broader ecological amplitude than any other species of medium and large sized mammals in southeastern Alaska. Otters also have a greater ability to coexist intelligently with human presence and activities than does any other terrestrial

species. Genuinely commensal associations with human development, and perhaps with sea bird colonies, may be in evidence. If not affected destructively, otters will remain in their focal waters regardless of the degree of human competition.

The otters in these ranges exhibited extreme conservatism of range occupancy and resource exploitation, and changed very little over time regardless of the successional or other changes of the environment around them. Such changes may influence the pods to alter their patterns of activity, but not the nature of their activities.

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